

Anatomy of the Melanonidae (Teleostei: Gadiformes), with comments on its phylogenetic relationships

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SYNOPSIS. The osteology and part of the soft anatomy of the gadiform family Melanonidae, represented by the genus *Melanonus* Günther, 1878, is described. *Melanonus* has several derived (autapomorphic) sensory features but only three osteological ones. Although contained within the Gadiformes the family is excluded from both the Macrouroidei and Gadoidei in lacking a modified palatine and enlarged intercalar and thus represents their sister-group designated as the Melanonoidei. The Suborder Gadoidei now comprises two families of uncertain phylogenetic affinity (Bathygadidae and Steindachneriidae) and two Superfamilies, Moridoidea and Gadoidea.

INTRODUCTION

The gadoid genus *Melanonus* Günther 1878 contains two species, *M. zugmayeri* Günther, 1878 (Fig. 1), and *M. gracilis* Norman, 1930, which together give a broad latitudinal, circumglobal distribution (Cohen et al., 1990; Howes, 1991a). *Melanonus* are relatively small fishes, the largest seen being 230mm total length and, oddly for gadoids, are meso-bathypelagic (100–3000m). Outwardly, *Melanonus* resembles a stomiatoiid rather than a gadoid fish with its dark coloration, large, strongly-toothed jaws and tapering body (Fig. 1).

Until Marshall (1965) recognised (without diagnosis) a separate family for the genus, *Melanonus* had been considered to belong to the Moridae. Marshall (1965) and Marshall & Cohen (1973) contended that *Melanonus* was the most primitive gadiform (anacanthine) fish, a contention based on

the posterior position (at the forebrain) of the olfactory bulbs and a relatively unmodified caudal fin skeleton. The features Marshall & Cohen (1973) used to diagnose the Melanonidae rested on soft anatomical features, viz. an elaborate system of free ending neuromasts on the head and the corpus cerebelli extending (forward) to the optic tectum.

Apart from a few observations on the caudal fin skeleton and gill-arches and a description of its cranial muscles (see below) the anatomy of *Melanonus* has never properly been described. Gosline (1971) complained that “No account of the osteology is available. By contrast the family Gadidae has received more attention from anatomists than almost any other family of fishes”. Despite these shortcomings several assertions as to the phylogenetic position of the Melanonidae have been made.

Rosen & Patterson (1969) cited Marshall (1965; 1966) to the effect that *Melanonus* represents a primitive gadoid.



Fig. 1. *Melanonus zugmayeri* specimen BMNH 1991.7.9:729–30, 200mm SL, lateral view.

Schwarzahns (1980; 1984) combined the Melanonidae and Moridae (produced as a cladogram in Patterson & Rosen, 1989) and Cohen (1984) and Fahay & Markle (1984) also suggested a relationship with the Moridae, again based on the primitive arrangement of the caudal fin skeleton. Markle (1989) revised his earlier views and placed the Melanonidae near the base of his cladogram making it (with the exception of the Ranicipitidae) the sister group of all other gadiforms. Nolf & Steurbaut (1989) placed Melanonidae as an unresolved polychotomy with the Eulichthyidae, Macrouridae, Moridae and other gadoids. Okamura (1989) omitted the family from his gadoid classification but implied (p.137) on the basis of similar anterior rib structure that *Melanonus* is closely related to *Merluccius*. Howes (1989; 1990) also placed Melanonidae in an unresolved polychotomy, with Steindachneriidae, Bathygadidae and other gadoids. According to Howes (1990, 1991a & b) the majority of gadoid families form a monophyletic assemblage termed 'supragadoids', characterized by complete fusion of the upper hypurals into a single plate. The Macruronidae represent the plesiomorphic lineage of this assemblage with the Gadidae and Merlucciidae being the most derived families. The Melanonidae was assigned with the Bathygadidae, Steindachneriidae, Moridae and Eulichthyidae to the 'infragadoids' and in one scheme (Howes, 1991b) in alternative positions, one as the sister group to all gadoids excluding the Bathygadidae and Steindachneriidae, the other as also excluding the Moridae. The characters on which these phylogenetic positions were based are, however, ambiguous (see Discussion) and like all previous studies have suffered from lack of anatomical information about *Melanonus*. The following is an account of the osteology and other soft anatomical features of *Melanonus*.

MATERIALS AND METHODS

Specimens used for anatomical descriptions (all from BMNH collections): *Melanonus zugmayeri* Ucat. 230mm, 'Discovery' Stn 11550, 10.VII.1987, 20°25.5'N, 19°39.5'W, 775–825m; 1991.7.9:729–730, 220mm, 95mm SL, 20°25.8'N–31.4'N, 19° 39.8'W–38.0'W, 800–875m; 1991.7.9:731–733, cleared & stained, 66, 100, 130mm SL, 17°1.2'N, 19°57.8'W, 400–495m; 1987.1.21:595–596, 215mm

SL, dry skull prepared from 190mm SL, 49° 21.9'N, 11°51'W, 1090–1100m; 1987.1.21:597, 168mm SL, S.W. Bantry, 960–920m; 1981.3.16:377, 173mm SL, West Great Sole Banks; 1987.1.21:598–601, 175, 187, 193mm SL, one specimen, 165mm SL (cleared and stained), 50°02'N, 11°22'W, 910–980m; 1930.1.12:943 (Holotype) 13°58'S, 11°43'E. *Melanonus gracilis* 1887.12.7:22 (Holotype) 147mm SL, Antarctic; 1930.1.12:934–936, 97, 140, 150mm SL, 46°56'S, 46°03'W; 1988.11.4:13–20, 45, 49mm SL (cleared and stained), 35°13'–34°57'S, 17°50'–17° 48'E; 1988.11.4:2, 145mm SL, 50°17.7'S, 18°40.9'E, 300–150m; *Percopsis omiscomayus* 1973.3.20:46–8, 52mm (cleared and stained), 62mm SL, Lac Henry, Quebec, Canada; *Bregmaceros* sp. 1957.12.2:5–12, 54mm SL (cleared and stained) Senegal; *Gaidropsarus mediterraneus* Ucat. 122, 145mm (cleared and stained), Seaton Point, England.

In addition, material listed in Howes (1988, 1992) and Howes & Crimmen (1990) was re-examined.

Abbreviations used in the figures

aa	anguloarticular
aap	premaxillary articular process
ac	actinost
afc	anterior frontal crest
ap	premaxillary ascending process
ar	anterior ('chopstick-like') ribs
ard	anal fin radial
asp	autosphenotic
bb	basibranchial (numbered)
bh	basihyal
bl	Baudelot's ligament
bo	basioccipital
boc	basioccipital condyle
br	branchiostegal ray
cb	ceratobranchial (numbered)
cc	cerebellar corpus
ccr	cerebellar crest
cfc	central frontal crest
cl	cleithrum
cm	coronomeckelian bone
co	coracoid
de	dentary
dex	dorsal section of <i>epaxialis</i> muscle
dhy	dorsohyal
dr	dorsal fin ray

drd	dorsal fin radial	pc	postcleithrum
eb	epibranchial (numbered)	pfc	posterior (diagonal) frontal crest
ebt	epibranchial toothplate	phy	posterohyal
ect	ectopterygoid	pmp	postmaxillary process of premaxilla
edd	<i>erector</i> and <i>depressor dorsalis</i> muscles	pop	preopercle
ent	entopterygoid	pp	parapophysis
ep	epural	prn	prootic notch
epr	epineural	ps	parasphenoid
esc	extrascapular	psl	parasphenoid ascending laminae
epo	epioccipital	pte	pterotic
exc	exoccipital condyle	pts	pterosphenoid
exca	exoccipital cartilage	ptt	posttemporal
exf	exoccipital flange	pu	preural vertebra (numbered)
exo	exoccipital	pyc	pyloric caeca
fIX	foramen for glossopharyngeal nerve	qu	quadrate
fX	foramen for vagus nerve	ra	retroarticular
fl	facial lobe	Rel	ramus canalis lateralis nerve
fm	foramen magnum	rd	<i>retractor dorsalis</i> muscle
foc	foramen for occipital nerves	re	rostrodermosupraethmoid
fr	frontal	sb	swimbladder
fv	<i>flexor ventralis</i> muscle	sbp	swimbladder pocket
fvi	<i>flexor ventralis inferioris</i> muscle	sc	scapular
ge	granular eminence	sca	<i>supracarinalis anterior</i> muscle
gg	gas-gland	scl	supracleithrum
go	gonad	so	supraoccipital
gu	gut	sop	subopercle
ha	haemal arch	spt	intercalar socket for posttemporal limb
hb	hypobranchial (numbered)	st	stomach
hf	hyomandibular fossa	sy	symplectic
hp	hypophysis	ul	ural centrum
hy	hypural (numbered)	v	vertebra (numbered)
iac	interarcular cartilage	vex	ventral section of <i>epaxialis</i> muscle
ic	intercalar	vhy	ventrohyal
ih	interhyal	vo	vomer
io	infraorbitals (numbered)		
iop	interopercle		
ird	<i>interradialis</i> muscle		
ki	kidney		
le	lateral ethmoid		
li	liver		
llp	lateral ethmoid-palatine ligament		
lmi	mandibular-interopercular ligament		
lt	trigeminal lobe		
mc	Meckel's cartilage		
md	mesonephric duct		
mec	mesethmoid cartilage		
met	metapterygoid		
mss	myoseptal strands supporting ribs		
mo	medulla oblongata		
nI-VII	cranial nerves		
na	nasal		
na1	first neural arch		
naap	nerve branch serving <i>adductor arcus palatini</i> muscle		
nau	acoustic nerve		
nbuc	buccalis branch of trigeminal trunk		
nio	infraorbital branch of trigeminal trunk		
nll	lateral line nerve		
nm1,2	neuromasts types 1 and 2		
nnm	nerve of supraorbital branch innervating posterior canal enclosed neuromast		
nr	nasal rosette		
nsab	supraorbital branch of trigeminal		
ob	olfactory bulb		
op	opercle		
ot	olfactory tract		
pa	parietal		
pah	parhypural		
pal	palatine		
pb	pelvic bone		
pbb	pharyngobranchial (numbered)		

ANATOMY

Neuromast pattern (Fig. 2).

Melanonus has a unique pattern of free-ending neuromasts covering the head in addition to those more usual neuromasts contained in the sensory canals. There are two morphotypes of the former: 1) the most numerous, are long, flange-like structures which occur on the skin covering the upper rim of the infraorbitals, the snout, cheek muscles, preoperculum and top of the head; 2) button-like structures confined to specific areas on the lower cheek, snout and frontal.

The flange-like neuromasts are usually arranged longitudinally and more or less in rows. In the snout region, individual neuromasts may be slightly curved or angled to the general direction of the others (Fig. 2B). On top of the head, rows are more definite and those on the snout tend to converge anteriorly where the organs close to the midline are larger than the others (exceptional is the star-shaped arrangement posterior to the medial extrascapular sensory pore in *M. zugmayeri*); the neuromasts close to the midline on the central part of the frontal are also nearly twice the length of the others (Fig. 2A). In *M. zugmayeri* the neuromasts along the anterior part of the supraoccipital have a regular arrangement (Fig. 2A) but in *M. gracilis* they form a pocket or enclosed area. Distribution on the preoperculum is irregular and sometimes sparse (the skin is often missing from this region and it is not possible to make precise counts).

The pitlines of button-like organs are in a double row near the border of the snout, in a patch above the nares, as an

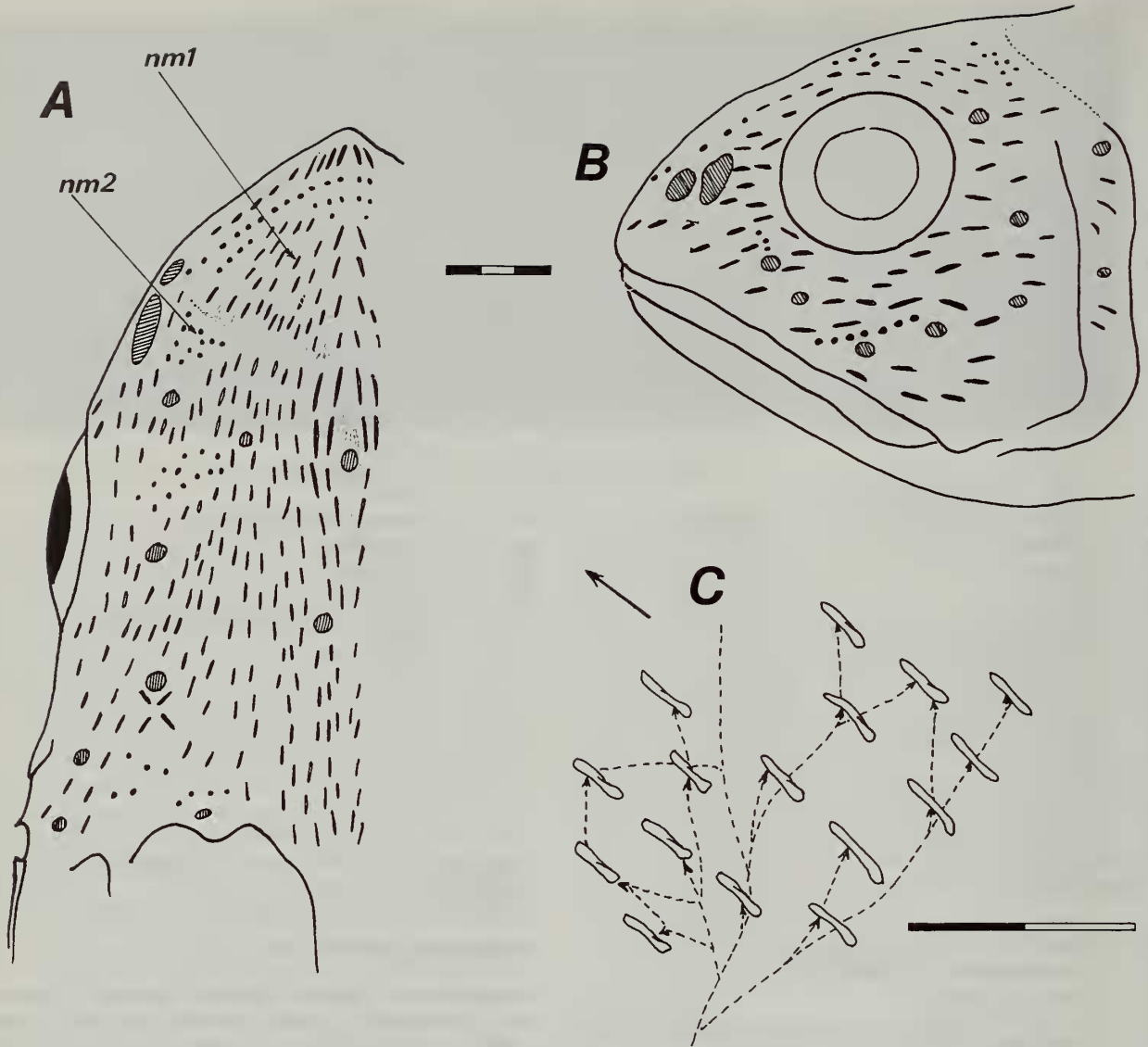


Fig. 2. Distribution of neuromasts types 1 and 2 in A, *Melanonus zugmayeri* on dorsal surface of head and B, *M. gracilis* on lateral surface of head. C, innervation pattern of type 1 neuromasts in subnasal region (right side) of *M. zugmayeri* (dashed lines indicate nerves, arrow heads indicate termination of nerve branch; large arrow points anteriorly). In this and subsequent figures, scale bars in millimetre divisions.

oblique row across the lower part of the cheek and a double row across the epioccipital region (Figs 2A,B). The neuromasts do not extend backwards on to the body.

There are about 500 flange-like neuromasts covering the entire head. Innervation is by the ramus canalis lateralis (Rc1 *sensu* Freihofner, 1970) which exits from the posterior frontal foramen to anastomose through a loose fascia of connective tissue. The neuromasts are innervated by subbranches stemming from a complex nerve network (Fig. 2C).

The Rc1 nerve branches from the supraorbital trunk of the trigeminal complex, (Fig. 17), a condition similar to that in *Merluccius* (Freihofner, 1970). The branch innervating the large posterior neuromasts enclosed in the frontal sensory canal detaches separately from the supraorbital trunk, whereas in *Merluccius* the nerves separate off together.

The large, plate-like neuromasts, housed in the sensory canals number two in the nasal bone, three in the frontal (one beneath the anterior medial ridge, one beneath the lateral arch and one posteriorly), one in the anterior part of the

pteroptic, one in the parietal, one in each extrascapular, three in the first infraorbital, one in the second, third and fourth, two in the fifth and one in the sixth, and five in the preoperculum.

Infraorbitals (Fig. 3).

There are six infraorbital bones, the first long and relatively deep with a broadly fretted ventral border, the outer flange which forms the roof to the sensory canal extends as a shelf along the anterior half of the bone, but curves laterally along the posterior half. The ascending process which contacts the posterior wall of the lateral ethmoid is tall and spine-like. The second infraorbital is confluent with the first and is as deep but only a sixth of its length. The medial lamina of the third is widely separated from that of the second although the dorsolateral flange is nearly in contact. The third together with the fourth form the posteroventral corner of the orbit and the fourth has only a short orbital margin and flange

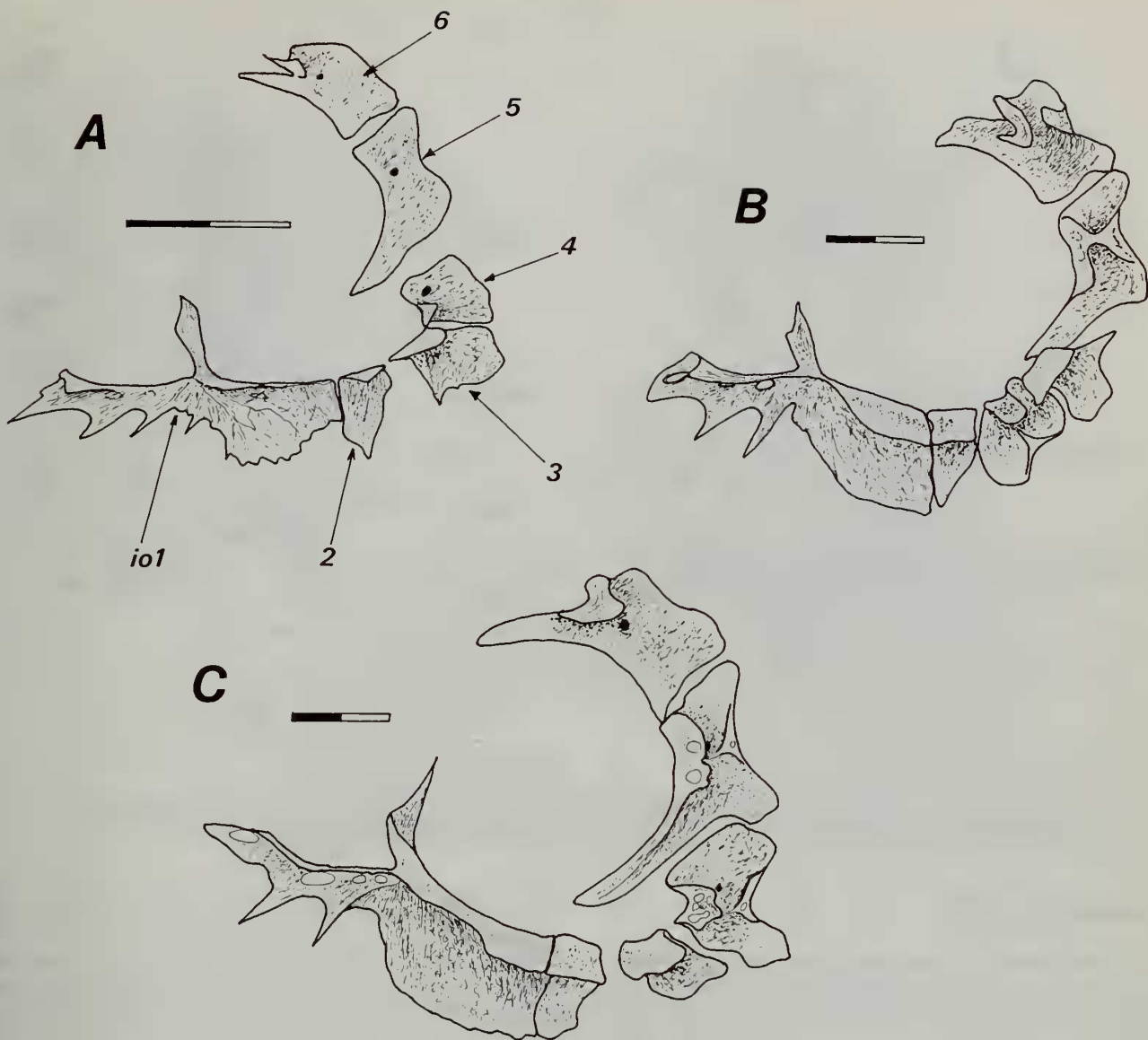


Fig. 3. Infraorbital bones of *M. zugmayeri* in specimens of: A, 66mm SL; B, 100mm SL and C, 130mm SL.

posteriorly, the body of the bone is expanded. The fifth infraorbital has a long orbital margin, the lower part of which projects anteroventrally in front of both the third and fourth to which it is connected by strong connective tissue; it has a narrow flange along its upper orbital border. The sixth (dermosphenotic) is as large as the fifth and has a pronounced orbital curvature which brings its anterior tip to the same vertical plane as the ascending process of the first infraorbital.

In the two smaller specimens of *M. zugmayeri* examined, the dorsolateral flange remains undeveloped on the first, fifth and sixth infraorbitals of the 66mm specimens and the ascending process of the first infraorbital is inclined anteriorly in both (Fig. 3A). The anteroventral border of the fifth infraorbital is less pronounced and in the 100mm SL specimen its tip lies medial to the rim of the fourth infraorbital; the sixth lacks the anterior elongation of the larger (130mm SL) specimen (Figs 3B, C).

Unlike other gadiforms where the posterior (fifth and sixth) infraorbitals are shallow, those of *Melanonus* are as deep as the anterior ones. The anterior curvature of the upper infraorbital (dermosphenotic) is more reminiscent of some macrouroids (see below) than gadoids. The central position of the ascending process of the first infraorbital is probably a plesiomorphic gadiform feature (on the basis of commonality) as is the reduced size of the second infraorbital. The extension of the lower part of the fifth infraorbital and the enlargement of the dermosphenotic are, because of their restricted distributions, taken to be derived features. According to Iwamoto (1989) among macrouroids, exclusion of the third and fourth infraorbitals from the orbit is a derived condition. In *Melanonus* similar exclusion has resulted from ventral extension of the fifth infraorbital whereas in the macrouroids illustrated by Iwamoto (1989, fig. 5G) it is due to re-alignment of the fourth infraorbital which covers the orbital borders of the second and third.

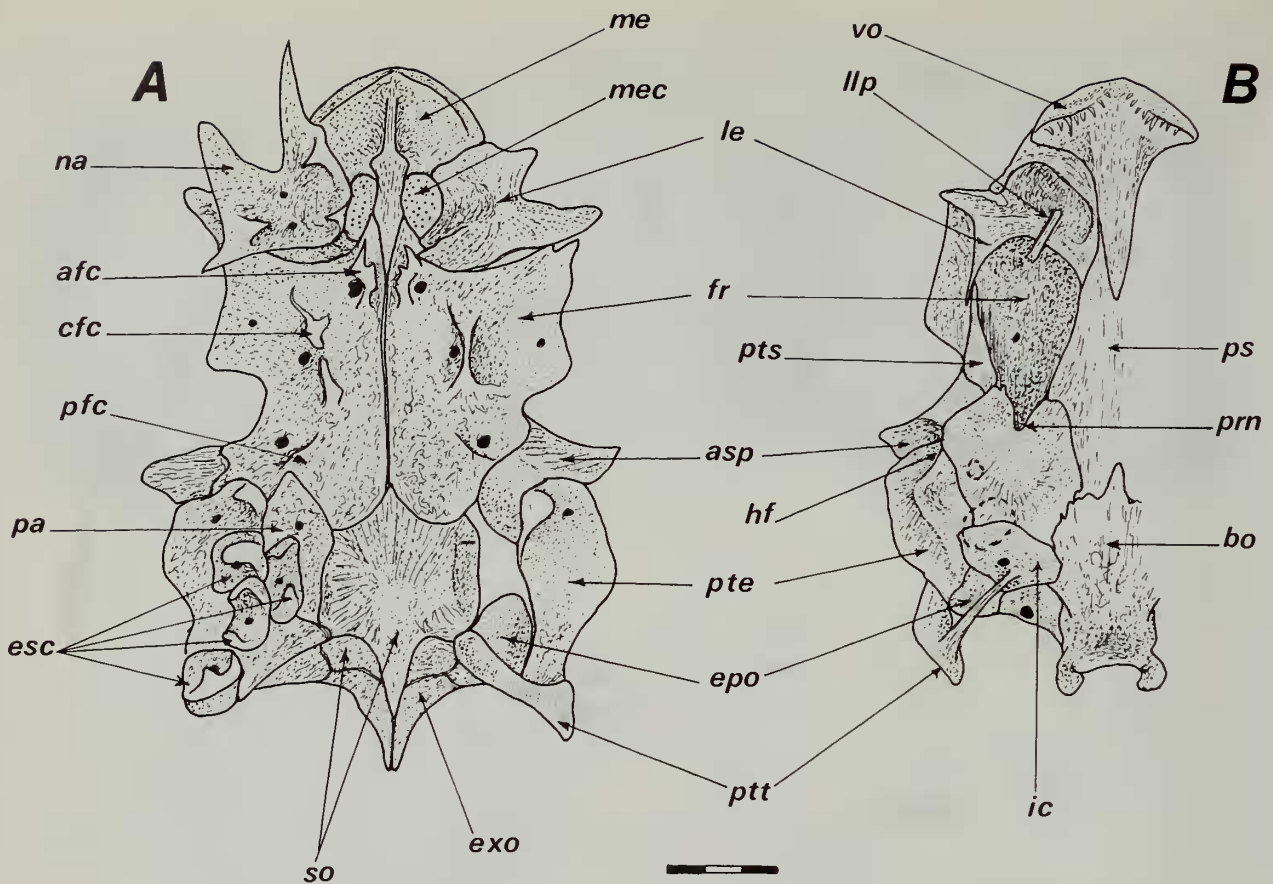


Fig. 4. Neurocranium of *M. zugmayeri* in A, dorsal and B, ventral views. In A, the right parietal, right nasal and left posttemporal have been removed. In B, dashed outline circles on the prootic and intercalar indicate the positions of the otoliths.

Cranium (Figs 4–8).

In its overall shape the cranial roof is almost square, the most noticeable feature being the deep indentation of the lateral frontal border anterior to the sphenotic, and the prominent anterolateral projections of the lateral ethmoid wings (Fig. 4A).

The *ethmoid* dorsal surface (rostrodermosupraethmoid) is, in keeping with that of other gadoids (Howes & Crimmen, 1990: 166), being narrow and cruciform with a steep anterior slope (Fig. 5B). The ossified anterior wall of the ethmoid forms most of the nasal cavity and a thin, vertical septum of ethmoid cartilage separates the cavities medially. A shallow bed of cartilage separates the base of the ethmoid and the vomer. The *vomer* has a thick, broadly rounded head bearing on either side 6 or 7 teeth in smaller specimens and 10–12 in larger (Figs 4B, 6A). In smaller specimens of both species the teeth are more or less arranged in a single row but in larger specimens the posterior teeth tend to be in a patch with one or two stout and caniniform being almost twice the length of their neighbouring teeth and three times that of the symphyseal teeth (Fig. 6A). The vomerine shaft is relatively short, extending to just beyond the posterior level of the lateral ethmoid. The base of the *lateral ethmoid* is long and broad and where it meets the vomer bears a deep cavity into which inserts the palatine ligament. The wall of the lateral ethmoid is thin and projects forward at an angle of 45°. The postero-

medial wall extends backward to directly contact the pterosphenoid.

The *nasals* (Fig. 4A) are large, almost entirely covering the lateral ethmoid and are narrowly separated from one another in the midline by the rostrodermosupraethmoid. Each bone has prominent anterior and posterolateral processes, two dorsal processes, lateral and medial, are folded inward to form curved flanges which support the skin roofing the sensory canal. In large specimens the nasals tend to become narrow with attrition of the anterior process (Fig. 6B).

The *frontals* are nearly square except that the posterior half of the lateral border is deeply indented. Anteriorly, close to the midline is a high, arch-shaped crest (afc, Fig. 4A), a similar but longer arch is situated in the centre of the bone and is sometimes divided into two separate crests (cfc, Figs 4A, 5B), posteriorly is a low, diagonal crest (pfc, Fig. 4A). All these crests shelter a neuromast foramen and serve to support the skin covering the frontal canal system. Posteriorly, the frontal margin meets the pterotic, is overlapped by the parietal and partially overlaps the anterior border of the supraoccipital. There are no ventral frontal laminae. The *parietals* (Figs 4A, 5B) are thin, near-diamond shaped bones each with a single neuromast foramen and posterolaterally covered by the median extrascapular. There is no parietal crest.

The *autosphenotic* (Figs 4A,B, 5B) has a prominent, bluntly rounded lateral process and is overlapped by the

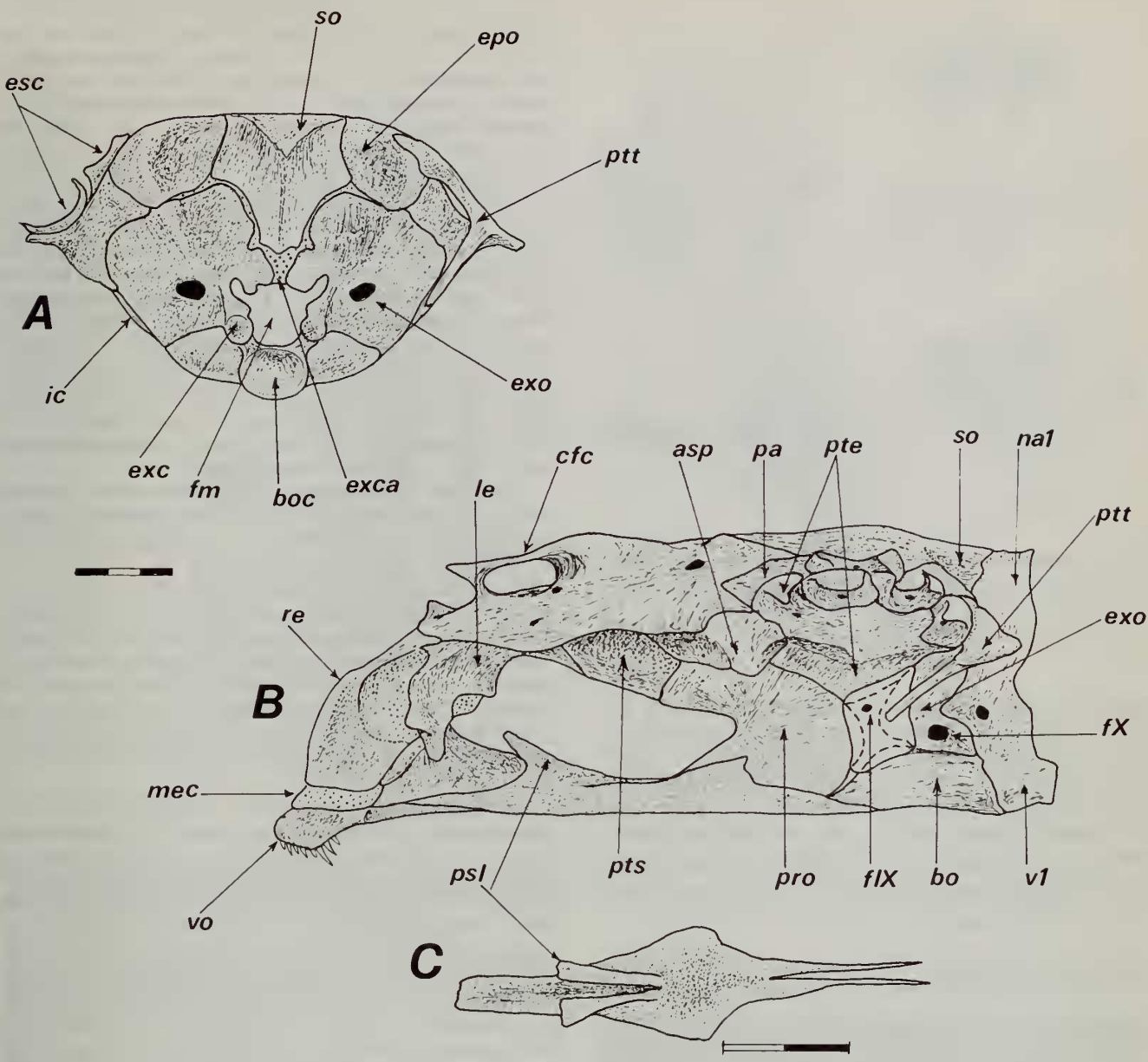


Fig. 5. Neurocranium of *M. zugmayeri* in A, posterior and B, lateral views. In B, the intercalar is unshaded, the margins of the bones underlying it indicated by dashed lines. C, parasphenoid of 66mm SL specimen in dorsal view.

frontal, parietal and pterotic. The underside of the bone bears a deep, almost transverse fossa into which articulates the hyomandibular. The *pterotic* (Figs 4A,B, 5A,B) accommodates the posterior portion of the hyomandibular fossa along a third of its lateral border. The wall of the pterotic is somewhat bullate and its cranial surface forms a prominent lateral shelf.

The *pterosphenoid* (Figs 4B, 5B) is long and deep forming most of the dorsomedial wall of the orbit, anteriorly it contacts the frontal and posteriorly the autosphenotic and prootic. The *parasphenoid* (Figs 4B, 5B,C) has a broad keel with, extending from its centre, a long, low ascending process which extends laterally at a low angle to the horizontal plane to meet the prootic; paired, parallel laminae rise from the central region of the keel to meet the bases of the lateral ethmoid wing (Fig. 6).

The *prootics* (Figs 4B, 5B) are large with a deep trigeminal notch. The posterior border of the bone is rounded and partially overlapped by a relatively small, ovoid *intercalar* to which is attached the inferior limb of the posttemporal (Figs 4B, 5A,B, 6D). The small, pinnacle-like *epioccipitals* contact the posterolateral margins of the supraoccipital and posteriorly the dorsal borders of their respective exoccipitals; laterally each epioccipital is overlain by the second extrascapular (Fig. 4A).

The *exoccipitals* are deeply depressed posteriorly and contain a large, backwardly facing vagus foramen (Figs 5A,B, 7). Medially, the bones meet across the midline by flange-like projections. Posteriorly there is an ovate, cartilage-filled process the base of which meets its antimeres in the midline. Inside each exoccipital a long, ventrally directed process extends from the medial surface to contact a shallow dorsal

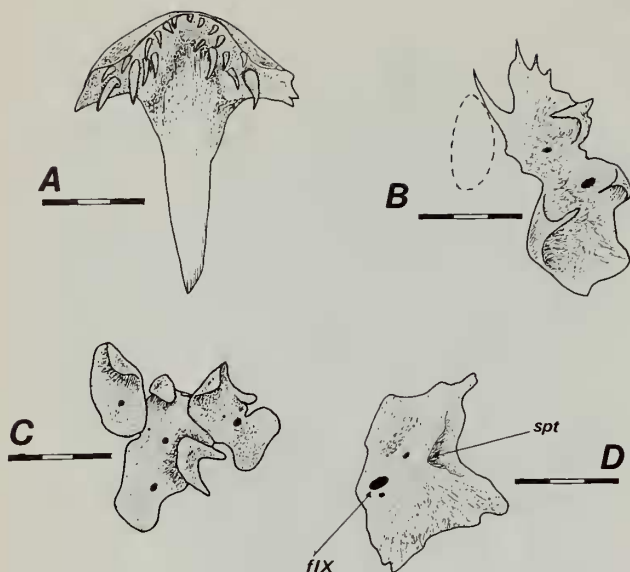


Fig. 6. *Melanonus zugmayeri*: A, vomer in ventral view; B, nasal of left side in dorsal view (broken outline indicates anterior nasal opening); C, extrascapulars of left side in lateral view; D, intercalar (left, lateral view). All from a specimen of 173mm SL.

flange rising from the base of the basioccipital (Fig. 7B). The *basioccipital* is a trowel-shaped bone the blade of which forms the posterior basicranium and the handle, the occipital condyle (Figs 4,5,7). The *supraoccipital* (Figs 4A, 5A,B, 7) is well-ossified and lies flush with the frontals, its crest confined to its posterior margin; laterally, the bone is bevelled where it meets the parietal. Posteriorly its ventral margin is bordered by the exoccipital.

The *otoliths* have been described and figured by Nolf & Steurbaut (1983; 1989).

Comments on cranial features

Melanonus has a plesiomorphic ethmo-vomerine region, namely a broadly rounded ethmoid lacking any dorsal elevation as in macrouroids and with a single, narrow point of contact with the lateral ethmoid (Howes & Crimmen, 1990; a more extensive area of contact appears to be a feature of some supragadoids, Howes, 1990); a laterally expanded lateral ethmoid which contacts the ascending process of the first infraorbital ligamentously on its posterior face (Howes, 1987); vomer with a relatively short shaft and well-formed teeth (absence of vomerine teeth in Macrouroidei and some gadoids is considered independently derived; see Okamura, 1989; Inada, 1989; Howes, 1990). Ophidiiforms have as broad a variability of the ethmovomerine region as gadiforms but the lateral ethmoid is characterised by the presence of basal twin facets which firmly unite with the large palatine head. Furthermore, the lateral wing of the lateral ethmoid is usually reduced and feebly developed, but always has a lateral facet which articulates with the first infraorbital (Howes, 1992).

The frontals of *Melanonus* have a plesiomorphic gadiform morphology; both gadoid and macrouroid taxa bear frontal crests of varying development as do ophidiiforms and this

may be a 'paracanthopterygian' feature. Howes (1990:79) noted the lack of ventral frontal laminae in *Melanonus* and considered this a derived condition associated with the anterior displacement of the frontal area of the brain (see p.27). Ventral frontal laminae are widely distributed amongst ophidiiforms. There is no prominent V-shaped ridge pattern on the frontals in *Melanonus* and no 'mucosal' cavity, a feature of supragadoids.

Nasal bones are plesiomorphically separated in the midline but in macrouroids are joined for most of their lengths, a feature regarded as synapomorphic for the group (Iwamoto, 1989; Howes & Crimmen, 1990). Among gadiforms the size of the nasals is variable but they are nearly always large, trough-like bones containing two neuromasts. Among plesiomorphic gadoids (e.g. Bathygadidae) the size of the nasals approaches that of macrouroids but the bones remain separated along the midline. The melanonid condition is thus considered plesiomorphic although the nasal bones have a distinct apomorphic shape which more closely approaches that of some macrouroids than gadoids.

The pterotic of *Melanonus* has a plesiomorphic gadiform morphology and resembles that of Bathygadidae in being broad with a rounded posterior margin and short hyomandibular fossa (Howes & Crimmen, 1990, fig. 6).

The pterosphenoid is unusually large for a gadiform; the widespread condition (and among ophidiiforms) being small, occupying the dorsoposterior region of the orbit and widely separated from the lateral ethmoid. The enlarged anteriorly extended bone is therefore considered autapomorphic for *Melanonus*. The parasphenoid displays no particular derived feature and corresponds with the situation in the majority of gadiforms, namely a broad flat keel with parallel laminae (Howes, 1990:81).

The deeply incised trigeminal notch of the prootic resembles most closely that of some Phycidae and the Muraenolepididae, but unlike those taxa the anterior wall of the prootic is directed medially as in most infragadoids and macrouroids (Howes, 1990:82). The intercalar is small in comparison with that in other gadiforms where in gadoids it is exceptionally large covering the entire posterolateral cranial wall. A large intercalar is one of the characters diagnostic of paracanthopterygians but is secondarily absent in lophiiforms and batrachoidiiforms. Among ophidiiforms and percopsiforms the intercalar is generally not as large as that of gadiforms, and in those two former groups is confined to the upper half of the posterior cranial wall and does not extend ventral to the basioccipital anteriorly but is interrupted by the prootic.

The relationship between the epioccipital and supraoccipital is an unusual one amongst gadiforms in that the posterior walls of the exoccipitals meet across the midline and so exclude the supraoccipital from contributing to the upper margin of the foramen magnum. Elsewhere in paracanthopterygians this condition occurs among ophidiiforms (Howes, 1992) where the exoccipital has enlarged backward and upward to cover the posterior margin of the supraoccipital. Even in the largest cleared and stained specimen of *M. zugmayeri* examined for this feature the ventral tip of the supraoccipital does not reach the margin of the foramen magnum (Fig. 7B). The supraoccipital lacks a dorsal crest, there being a posterior lamina (Fig. 7). Howes (1990:82) discussed the variability of the supraoccipital crest amongst gadoids. An elevated cranial crest is possibly the plesiomorphic condition for paracanthopterygians but a low, reduced crest is widely distributed amongst all groups and in lophii-

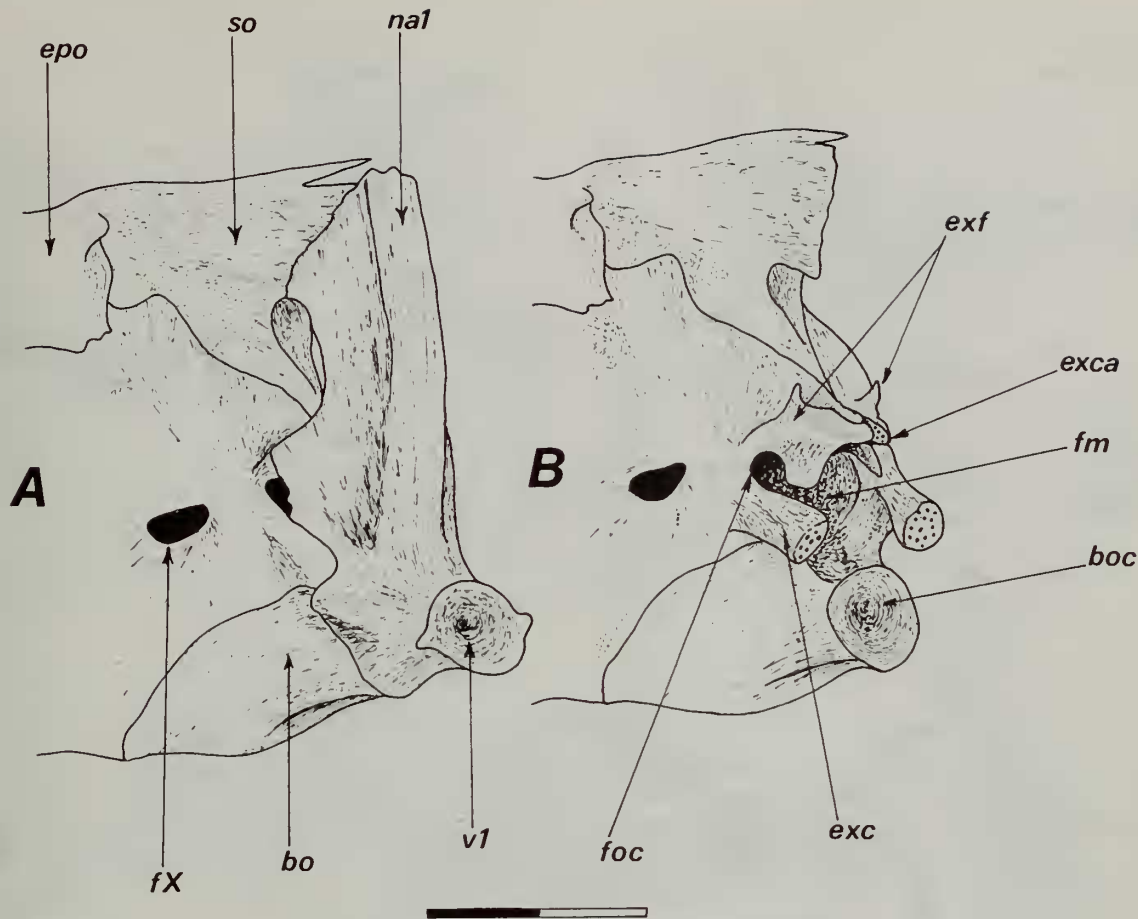


Fig. 7. *Melanonus zugmayeri* posterior part of cranium in lateral oblique view of 130mm SL specimen showing in A, first neural arch and vertebra attached and in B, removed to expose the posterior features of the basi- and exoccipitals. Note the supraoccipital does not contribute to the border of the foramen magnum.

forms and ophidiiforms appears to be the common condition. It is assumed that this feature has been repetitively evolved in these groups.

Jaws (Fig. 8)

The *premaxilla* (Fig. 8C) has tall, thin and widely separated ascending and articular processes, and a tall, spine-like postmaxillary process. The toothed surface is narrow, bearing for most of its length two rows of sharp pointed teeth. The outer row teeth are straight or extend slightly laterad, the inner row teeth which are about twice the length of the outer are inwardly curved; posteriorly there are three rows of teeth, the ones of the centre row being the same size as those of the inner (Figs 8D,E). In a 100mm SL specimen of *M. zugmayeri* the posterior teeth are so arranged as to form distinct transverse rows (Fig. 8F) but this is not evident in the 66mm or 130mm SL specimens. The *maxilla* has a tall articular head and a short medial articular process forming a rather acute angle with the head (Figs 8A,B). The shaft of the bone is slender and posteriorly bears shallow dorsal and ventral processes.

The *dentary* (Fig. 8G) is short and deep with a corresponding shallow mentomeckelian cavity; it has a high steep coronoid process. The sharp pointed teeth are set in an

irregular single row, numbering 22 in 88mm and 100mm SL specimens of *M. zugmayeri*, 28 in a 130mm and 34 in a 175mm SL specimen. The anterior teeth are small followed by four or five successively larger ones, then four or five relatively large teeth separated by three or four smaller ones. Posteriorly the teeth diminish in size. The *anguloarticular* (Fig. 8G) is tall with a steep posterior slope and short, vertical anterior margin; the articular condyle is long and narrow. The *coronomeckelian bone* (Fig. 8G) is a well-developed, cylindrical element with slight dorsal and ventral posterior flanges. The *retroarticular* (Fig. 8G) is boot-shaped, the leg being curved forward and the foot long and shallow. A strong labial ligament is anchored to the rim of the dentary (Howes, 1988, fig. 12).

The overall jaw morphology of *Melanonus* is plesiomorphic for gadiforms, the upper jaw bones, apart from having a smaller postmaxillary process of the premaxilla, are little different from those in bathygadids (Howes & Crimmen, 1990). Macrouroids are characterised by having a large postmaxillary process of the premaxilla situated posteriorly (Okamura, 1970; Howes & Crimmen, 1990). There is no 'gadoid notch' at the base of the postmaxillary process. The lower jaw more closely resembles that of gadoids or ophidiiforms than macrouroids in having a relatively shallow anguloarticular and boot-shaped or J-shaped retroarticular.

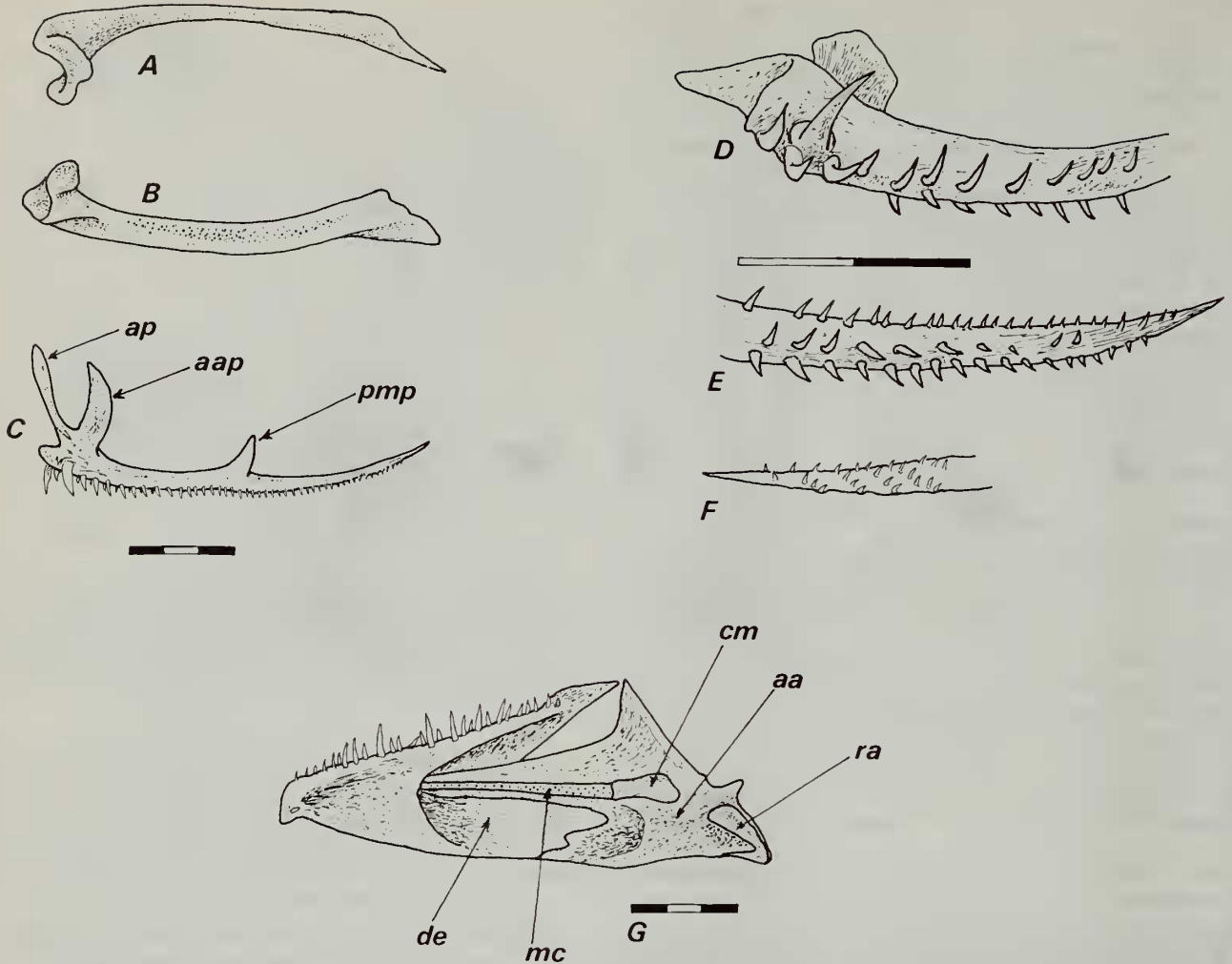


Fig. 8. *Melanonus zugmayeri*, jaw bones. A and B right maxilla from a 130mm SL specimen in: (A) dorsal and (B) medial and slightly ventral views; C, premaxilla in lateral view; D-F premaxilla, anterior (D) and posterior (E) regions from 130mm SL specimen and (F) 100mm SL specimen, ventral views; G, lower jaw of 130mm SL specimen in medial view.

Macrouroids tend toward a deeper anguloarticular and greater variability in the shape of the retroarticular (Okamura, 1970; Howes & Crimmen, 1990). A boot-shaped retroarticular is lacking in both percopsiforms and lophiiforms.

Palatopterygoquadrate (Fig. 9)

The *palatine* (Fig. 9A,B) is long, its posterior tip extending to nearly halfway along the ectopterygoid, its rostral process is long and slender and overlies the maxilla, its base bears a broad facet which articulates with the ethmoid cavity and the body of the bone rises to a high posterior crest. There are two rows of sharply pointed teeth.

The anterior part of the *ectopterygoid* (Fig. 9A) lies along the medial face of the palatine and its ventral stem reaches the quadrate joint; laterally it is slightly overlapped by the *entopterygoid* (Fig. 9A). The latter is a relatively large bone with a rounded dorsal profile and is sloped mesad, its posterior border is well separated from the hyomandibular by the *metapterygoid*. The *metapterygoid* (Fig. 9A) is axe-shaped its posterior margin rising high up the leading edge of the hyomandibular shaft.

The melanonid palatine is unique amongst gadiforms, in its length, nature of contact with the pterygoids, and in bearing teeth. The common condition, and one which is considered synapomorphic for gadiforms (p.29) is for the palatine to be reduced in length with a vertical or slightly angled posterior border meeting a similar blunt margin of the ectopterygoid and forming a hinge-type joint (see figures in Okamura, 1970, 1989; Howes, 1990, 1991b; Howes & Crimmen, 1990). This union differs from that commonly encountered in other paracanthopterygians where the posterior limb of the palatine is attenuated and articulates firmly with the leading edge of the entopterygoid and lateral face of the ectopterygoid. Percopsids resemble gadiforms in having a near vertical abutment of the palatine with the ento- and ectopterygoids (Fig. 9D). However, there is a posterior stem which overlaps the upper lateral margin of the ectopterygoid. Macrouroids are characterised by the lack of direct contact between the palatine and ethmovomerine bloc (Howes & Crimmen, 1990).

Norman (1930) noted there were 'teeth on the pterygoid', an error perpetuated by Howes (1991b, caption to fig. 35). The pterygoid bones of *Melanonus* display plesiomorphic morphologies; the large entopterygoid and high posterior

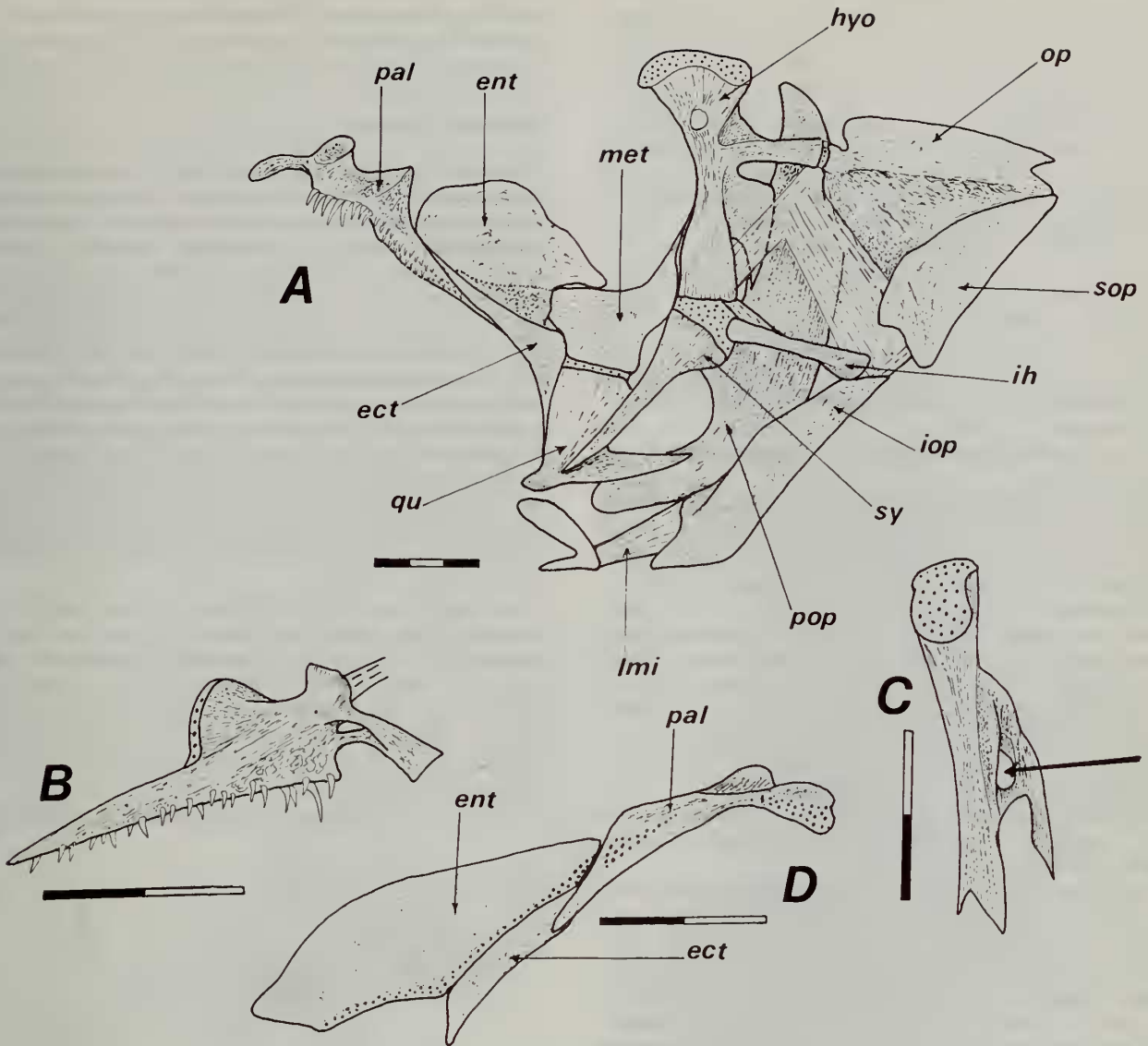


Fig. 9. A–C *Melanonus zugmayeri*: A, palatoquadrate, hyosymplectic and opercular bones of 130mm specimen in medial view, light hatched area represents ligamentous system connecting opercular bones to hyomandibular; B, palatine of 100mm specimen, right side, lateral view; C, hyomandibular, left side, of 100mm SL specimen in anterior view showing foramen for hyoid branch of facial nerve (arrowed) and lateral flange; D, *Percopsis omiscomayus*, palatine and pterygoids in lateral view (heavy dotting indicates cartilage).

metapterygoid process are present in macrouroids, bathygadids and macruronids (Howes & Crimmen, 1990; Howes, 1991b). Reduction of the entopterygoid and metapterygoid appears to be characteristic of supragadoids (Howes, 1990). Amongst ophidiiforms the metapterygoid abuts against the lower limb of the extended anterior portion of the hyomandibular.

The quadrate (Fig. 9A) of *Melanonus* has a wide angle between its posterior border and the posteroventral spine. The size of this angle is variable among gadiforms and appears correlated with the orientation of the suspensorium. An 'interosseous space' between the symplectic and preoperculum (Okamura, 1970; 1989) is also a condition of the angular separation of the two parts of the quadrate, being absent where the angle is small (Howes, 1990).

Hyoid arch (Figs. 9–11)

The hyomandibular (Fig. 9A) has, as in all gadiforms, a single articulatory condyle. The bone is narrow-waisted with the relatively long shaft oval in section, a foramen for the hyoid branch of the facial nerve pierces its posterior margin (Fig. 9C). Posteriorly is a long, horizontal process which articulates with the opercle. The lateroposterior face contacts the border of the preopercle. Medially a band of ligamentous connective tissue joins the shaft with the opercular process and a wider band runs at right angles to it to attach to the subopercle and interopercular-subopercular ligament (Fig. 9A).

The course of the hyoid branch of the facial nerve is partially exposed laterally, due to attrition of the outer part of the hyomandibular, part of which remains as a lateral flange which is a common feature (synapomorph) for gadiforms,

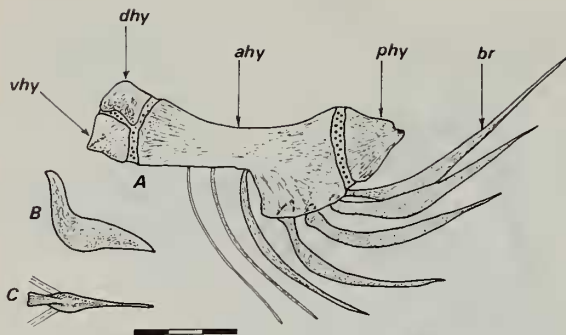


Fig. 10. *Melanonus zugmayeri* hyoid bar of 100mm SL specimen: A, medial view; B and C, urohyal in lateral and dorsal views.

one not shared by ophidiiforms or lophiiforms (Howes, 1992).

Other hyoid arch bones are much like those of the majority of gadiforms; the posterior half of the *anterohyal* = *ceratohyal auct.* (Figs 10A, 11A) is deep and in this respect resembles that bone in some macrouroids (eg. *Nezumia*, *Abyssicola*, *Coelorhynchus*, *Coryphaenoides*; Okamura, 1970), more closely than gadoids. However, this feature is variable and a similar range of morphotypes can be found among ophidiiforms (Markle & Olney, 1990, fig. 13). As in most gadiforms and ophidiiforms there are 7 *branchiostegal rays* which appears to be the plesiomorphic paracanthopterygian number, (six occur frequently in lophiiforms). The *urohyal* (Figs 10B,C) bears a closer resemblance to that of gadoids rather than macrouroids in having a shallow dorsal keel and a long, prominent anterodorsal (basibranchial) process (Howes, 1990, fig. 16B).

The *basihyal* (Fig. 11A) is a dumbbell-shaped bone lying between the dorsohyals and crossed by a ligament which connects them; anteriorly a thick cartilaginous 'tongue' protrudes forward, posteriorly, the basihyal is slightly overlapped by the first basibranchial (see below). The *interhyal* (Fig. 9A) is typically gadiform, being long and slender, contacting the symplectic cartilage dorsally and the posterior socket of the posterohyal ventrally. Markle (1989, fig. 6A) shows a common ligamentous connection between the interhyal-posterohyal and interopercle. I find this to be one involving thick connective tissue although a discrete ligament runs from the medial side of the interhyal to the medial posterior tip of the posterohyal.

Opercular bones (Fig. 9A)

The opercular bones are relatively generalised except that the suboperculum has a straight to concave leading edge rather than the common gadiform condition of a rounded to pointed margin. The *interopercle* is shallow and nearly oblong with rounded dorsoposterior and anteroventral borders; it is widely separated from, and ligamentously connected to the subopercle. In general, macrouroids have the interopercle orientated horizontally (e.g. Okamura, 1970, figs 26; 27) whereas in gadoids the bone is angled, sometimes steeply as in *Melanonus*. *Melanonus* lacks the interopercular fossa present in a subgroup of 'supragadoids' (Howes, 1990). The *opercle* is relatively large for a gadiform and overlaps most of the subopercle. The *preopercle* has a short lower, anteriorly directed limb and a narrow laminate (symplectic) process

which, plesiomorphically, contacts the symplectic cartilage. In its derived form the symplectic process of the preopercle contacts the lateral face of the hyomandibular (Howes, 1990).

Branchial arches (Fig. 11)

There are three *basibranchials* (Fig. 11A), the first and second ossified, the third cartilaginous. The posterior margin of the first overlies the anterior border of the diamond-shaped second which is separated from the small diamond-shaped third. The first and second *hypobranchials* (Fig. 11A) are long with marked posterior curvature, both contacting the first basibranchial and bear gill-rakers on their outer and inner margins; the third is short and lacks gill-rakers. The first and second *ceratobranchials* (Fig. 11A) bear five or six clustered-spinous rakers on their outer and the same number of slender, triple-spine rakers on their inner margins; the third has seven outer and inner shorter rakers and the fourth has four short rakers on its outer margin only. The anterior tips of the fifth ceratobranchials are apposed but not firmly united in the midline and are ligamentously connected to the third basibranchial; a narrow tooth patch bears ca 25 slender pointed teeth.

The *epibranchials* (Fig. 11B) are 30% the length of the ceratobranchials. A strong uncinuate process on the first epibranchial is connected by a chondrified ligament to a large interarcual cartilage; the third epibranchial bears a long tooth plate bearing ca 20 sharp pointed teeth. There are four *pharyngobranchials* (Fig. 11B), the first being an ossified element; the second-third pharyngobranchial tooth plates bear strong, pointed teeth.

Markle (1989) has described and commented on the upper

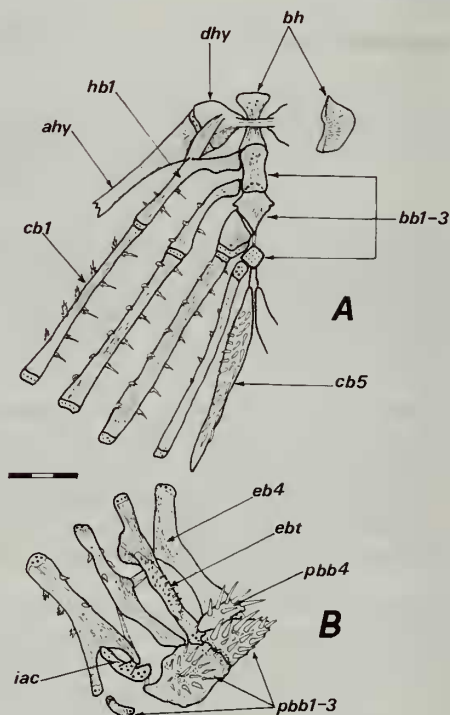


Fig. 11. *Melanonus zugmayeri* branchial arches of 130mm SL specimen: A, dorsal view of lower arch elements; B, ventral view of upper arch elements. In A, basihyal is also shown in lateral view.

branchial arch of *Melanonus* which he considers, due to the presence of a large and chondrified interarcual ligament, to be plesiomorphic for gadiforms. In his cladogram, however, he mistakenly ascribes to *Melanonus* the loss of the second pharyngobranchial. The lower gill-arch is also plesiomorphic in that the basibranchials are unexpanded and there is no forward ventral elongation of the third hypobranchial as in macrouroids and ophidiiforms; the first hypobranchial is typically long as in gadiforms but lacks an expansion where the ligament running to the dorsohyal attaches. Spinous gill-rakers of both the clustered- and triple-spine type are widespread amongst 'infragadoids' and macrouroids.

Pectoral girdle (Fig. 12)

The vertical and horizontal limbs of the *cleithrum* (Fig. 12A) are nearly equal in length; the medial cleithral lamina is thin and only prominent near the cleithral tip. Markle (1989) noted that the foramen which notches medial borders of both the scapula and coracoid is present only in the former (Fig. 12A). Markle (1989) and Howes & Crimmen (1990) commented on the variability of this feature; plesiomorphically the foramen lies entirely within the scapula, a condition

almost entirely confined to 'infragadoids' although it is also recorded in the 'supragadoid' *Lota*. The *supracleithrum* (Fig. 12B) is a lanceolate bone with a slightly expanded dorsal articular surface which contacts the posttemporal. There are four *actinosts* and 12 or 13 pectoral rays in the *M. zugmayeri* specimens examined (Norman, 1930, gives 13 for *M. zugmayeri* and 12-14 for *M. gracilis*; Fahay & Markle, 1984, give a range for the genus of 10-16). The single *postcleithrum* (Fig. 12A) has a broad head and slender, slightly upwardly curved stem. It articulates in a cleft opposite or slightly above the coracoid-scapula junction (see also Markle, 1989, fig. 10).

The *posttemporal* (Fig. 12B) is V-shaped, its upper limb broad proximally and tapering distally; its lower limb, which is firmly united with the intercalar is thin, rod-like and completely ossified.

The *extrascapulars* (Figs 4A, 5A,B, 6C) number four, each having upturned borders and containing a neuromast. The lateral extrascapular covers the posterior corner of the pterotic, two lie in contact with one another along the medial part of that bone and the innermost lies along the lateral part of the parietal. In large specimens of *M. zugmayeri* the

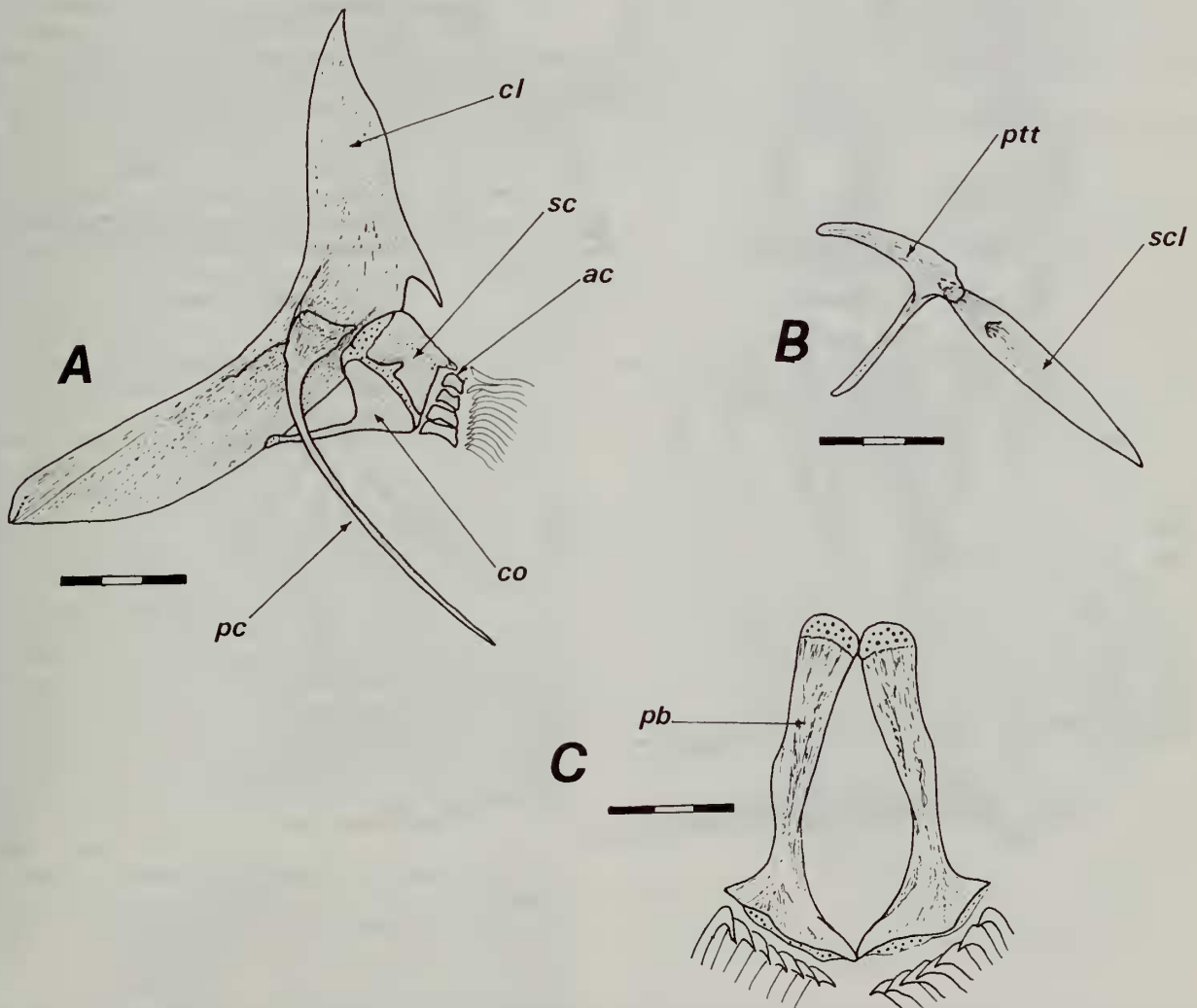


Fig. 12. *Melanonus zugmayeri*: A, pectoral girdle in medial view; B, posttemporal and supracleithrum in lateral views; C, pelvic girdle in dorsal view.

medial extrascapular is more closely aligned with the supraoccipital, resting along a lateral ridge of the bone and in a specimen of 173mm SL (Fig. 6C), it appears that the lateral and a medial extrascapular have become fused, judging by the presence of two neuromast foramina in the single large bone.

Pelvic girdle (Fig. 12C)

The pelvic bone is narrow and tubular, broadening proximally where its cartilaginous tip contacts its antimeric symphysially. Distally the pelvic process is narrow and straight and connected with its antimeric by ligamentous tissue. There is no lateral pelvic process or spine (cf. *Bathygadidae*, Howes & Crimmen, 1990). There are usually 7 fin rays; Fahay & Markle (1984) give a range for the genus of 5–7.

The pelvic girdle lies well forward with the anterior tips of

the pelvic bones lying between the cleithra so that the origin of the pelvic fin lies beneath or just anterior to that of the pectoral (Fig. 1). The position of the pelvic girdle in relation to the pectoral girdle is variable amongst gadiforms. In the majority of gadoids the pelvic girdle is situated well forward, particularly so in the more derived 'supragadoid' taxa such as gadids, gaidropsarids and muraenolepidids, so that the origin of the pelvic fin lies in advance of that of the pectoral fin. 'Infragadoids' tend to have the pelvic girdle situated beneath or behind the pectoral (e.g. bathygadids, steindachneriids). In morids, however, the pelvic girdle lies well forward. There is some variability in position among macrouroids but generally, the pelvic girdle lies posterior to the pectoral so that the origin of the pelvic fin is situated directly beneath that of the pectoral fin. With respect to the position of the pelvic fin relative to that of the pectoral, the *Melanonidae* appear to represent an intermediate condition between the derived forward and plesiomorphic posterior positions.

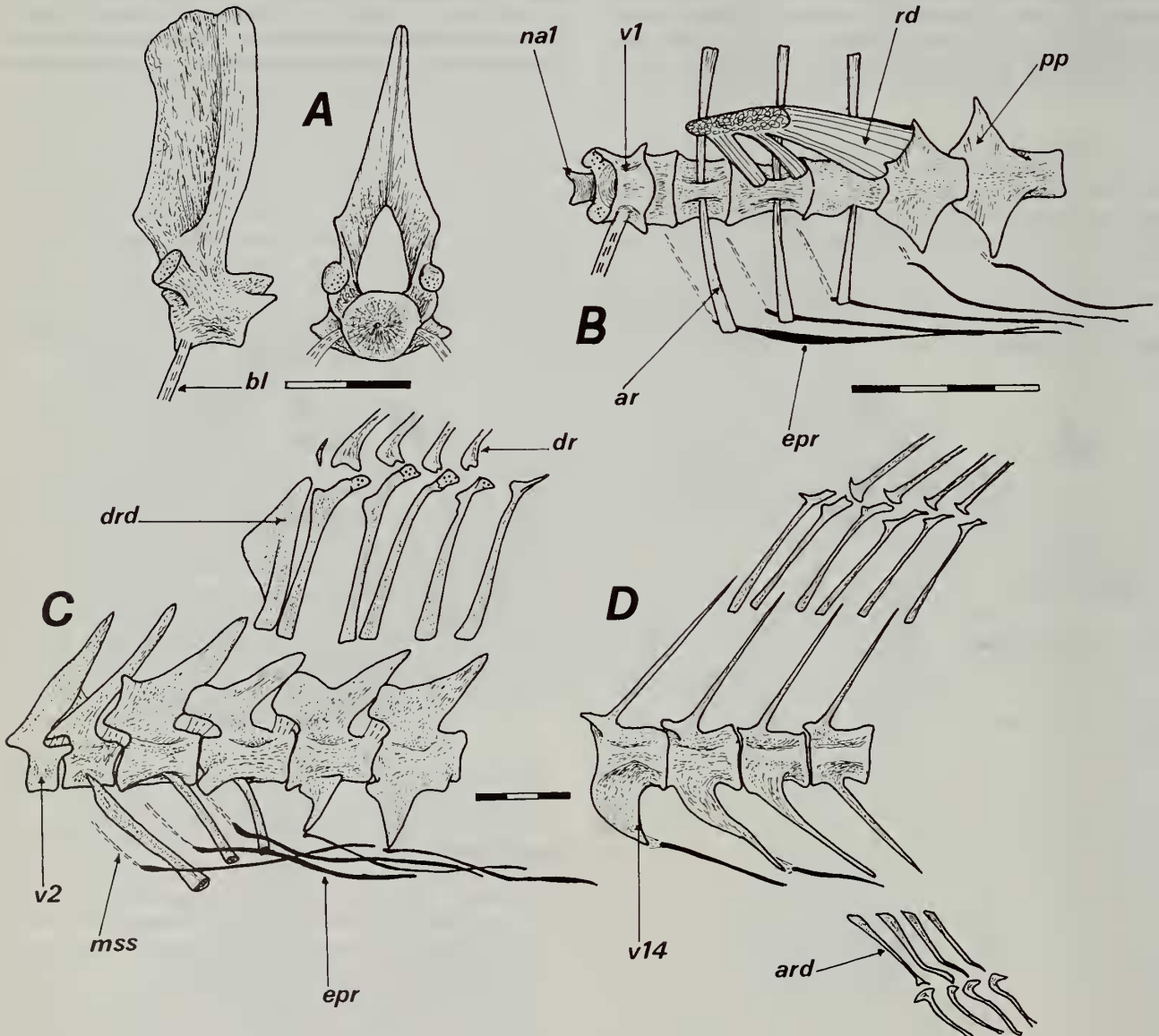


Fig. 13. *Melanonus zugmayeri* vertebral column. A, first vertebra and neural arch of 130mm SL specimen in lateral and anterior views; B, anterior part of vertebral column of 100mm SL specimen showing *retractor dorsalis* muscle of one side, in ventral view; C and D vertebral column and fin supports of 130mm SL specimen: C, anterior vertebrae, D, 14th-17th vertebrae showing anterior anal fin supports (lateral views; ribs shown in black for clarity).

Vertebral column and median fins (Figs 13–15)

There are 12–14 abdominal and 45 or 46 caudal (those with closed haemal spines) vertebrae in *Melanonus* (Fahay & Markle, 1984 give total counts of 58–62 for the genus). The first neural arch and spine are well-developed and form an ankylosed unit with the centrum. The prezygapophyses of the first vertebra (Fig. 13A) are oval in section, hollow and cartilage-filled and firmly in contact with the similarly shaped paired condyles of the exoccipital. The wall of the neural arch covers the upper posterior wall of the exoccipital leaving exposed a notch through which pass the occipital and lateral line nerves (Fig. 7B). The laminae of the neural arch extend forward to embrace the posterior extension of the supraoccipital crest (Fig. 7A). The second vertebra is anteroposteriorly compressed and lacks processes or ribs; the third-fifth vertebrae support successively shorter chopstick-shaped ribs which extend almost horizontally, at their tips lie epipleural (epineural) ribs the heads of which are ligamentously attached to their respective myosepta (Fig. 13B,C). The sixth-twelfth centra bear triangular parapophyses to each of which is attached a posteriorly curved epipleural rib. According to Okamura (1989) there is a total of eleven epipleural ribs in *Melanonus*; ten are counted here in *M. zugmayeri*.

There is a single *dorsal fin* comprising 72–78 rays. The first dorsal ray is often minute, the second and successive rays are long and flexible, supported by distally tapered rod-like radials which tend to occur in pairs within each interneural space, their proximal tips converging (Fig. 13C,D). The origin of the dorsal fin occurs between the third and fourth neural spines. There are no supraneurals (predorsals). The *anal fin* has 50–58 rays and lacks a stout anterior spine; the shape of the radials is similar to those which support the dorsal fin (Fig. 13D).

Caudal fin skeleton (Fig. 15A,B). The caudal fin skeleton of *Melanonus* resembles that of the Moridae in that the first and second hypurals are incompletely fused; each support a single fin ray. In morids all the hypurals are fused only proximally whereas in *Melanonus* fusion of hypurals 1 and 2 is both proximal and distal leaving a central opening (Fig. 15A). Hypurals 3–5 although fused in specimens of *M. zugmayeri* of 130mm SL are only partially fused in 66mm and 100mm SL specimens (Fig. 15B). Paulin (1983, fig. 5A) figures a caudal skeleton of *M. gracilis* in which hypurals 1 and 2 are entirely fused and the fifth is reduced. In a 45mm SL specimen of *M. gracilis*, all the hypurals are separated for their entire lengths whereas in a 49mm SL specimen they are fused distally but not proximally. There are two elongate epurals each supporting a fin ray; in a 100mm SL specimen of *M. zugmayeri* they are joined proximally (Fig. 15B). Unlike morids, *Melanonus* lacks X and Y bones a feature shared with Macruronidae, Gadidae and Lotidae. A long parhypural articulates basally with the fused hypurals 1 and 2 and supports a single fin ray.

Comments on features of the vertebral column and median fins. Chopstick-shaped ribs, similar to those of *Melanonus*, have been reported for *Macruronus*, *Lyconus*, *Steindachneria* and *Merluccius* by Okamura (1989) and Inada (1989) who arrive at opposite conclusions with regard to their character polarity. According to Okamura this rib-type suggests a close relationship between the taxa in which they occur. Inada, on the other hand, regards them as a plesiomorphic gadoid feature. Although Inada's (1989) reasoning appear to be

based on an *a priori* assumption of merlucciid plesiomorphy I would agree with his assumption. In fact, this type of rib is more widely distributed amongst gadoids than has been reported and also occurs amongst 'supragadoids' other than Merlucciidae (Fig. 14A).

In *Melanonus* the ribs occur on vertebrae 3–5 as in *Lyconus*, but they are on vertebrae 3 and 4 in *Macruronus* (both Macruronidae), 3–6 in Merlucciidae, and 3–4 in Gaidropsaridae. In Steindachneriidae the ribs are on vertebrae 3 and 4 but the rib on the fourth has less than half the thickness of that on the third whereas in the above cited taxa the ribs are of equal thickness. Furthermore, the epipleurals attach directly to the distal tips of the chopstick ribs in *Steindachneria* whereas in the other taxa they are indirectly attached by ligamentous strands running to the myosepta (as in *Melanonus*). In morids and 'supragadoids' epipleurals are attached directly to the vertebral ribs. Patterson & Rosen (1989) interpreted the vertebral ribs *Steindachneria* and *Gadus* as a parapophysis with attached epipleural. The ribs in Steindachneriidae, however, are like those of Melanonidae, Macruronidae and Merlucciidae in articulating with the ventral cavity of the centrum. In the Bregmacerotidae the third and subsequent vertebrae bear parapophyses to which are attached cartilage-formed ribs (Fig. 14B). The loss of epipleurals from the first and second centra is a gadiform synapomorphy (Markle, 1989).

Howes (1991b) regarded the first neural arch of *Macruro-*

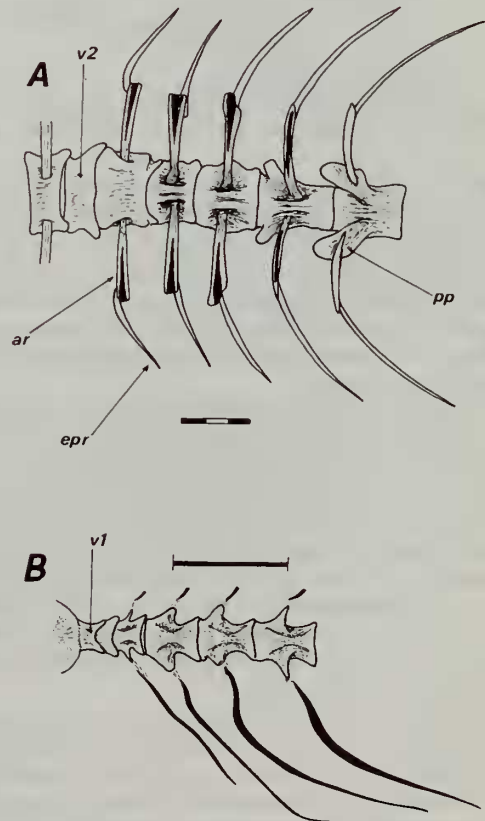


Fig. 14. Anterior region of vertebral column in: A, *Gaidropsarus mediterraneus*; B, *Bregmaceros* sp. In A, black shading in the ribs (ar) indicates zones of cartilage.

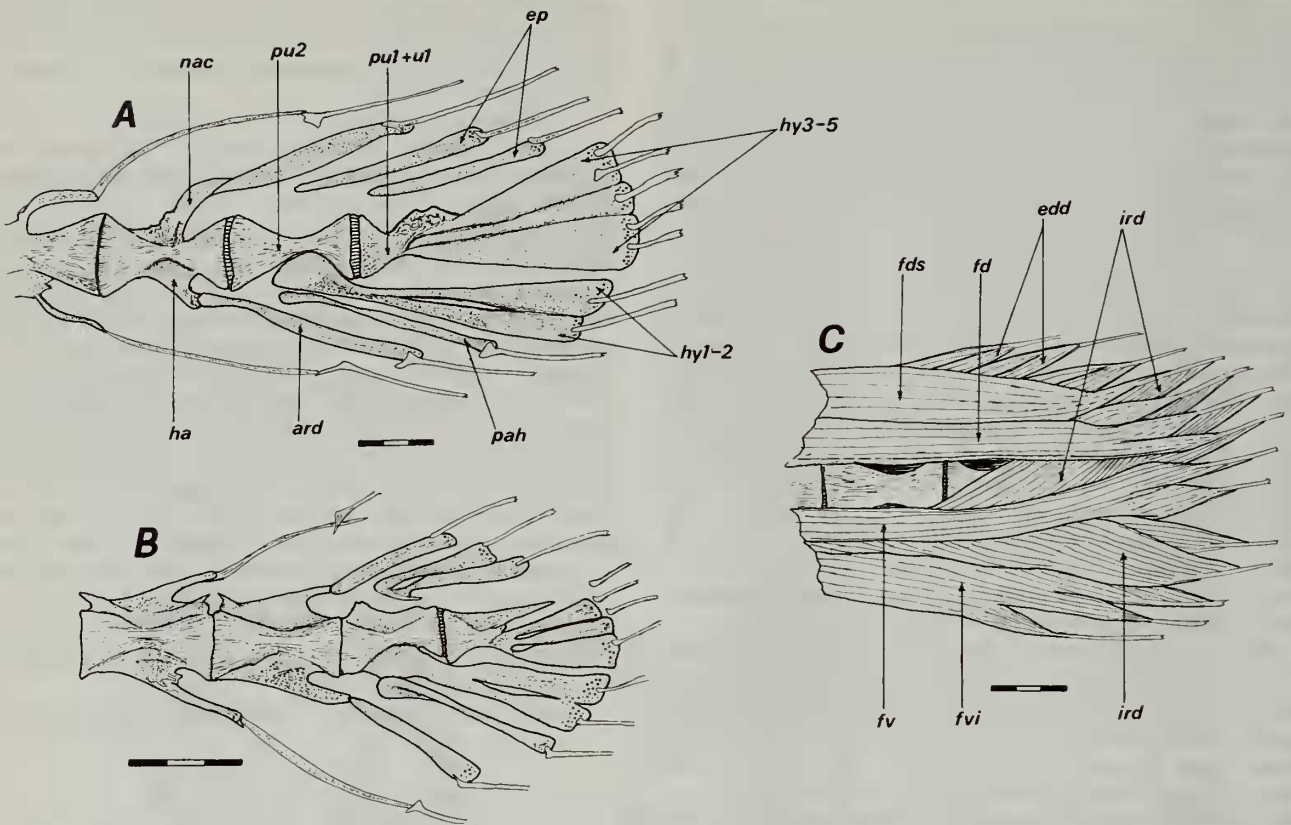


Fig. 15. *Melanonus zugmayeri* Caudal fin skeletons of A, 130mm SL and B, 100mm SL specimens. C, caudal fin musculature (although a superficial layer of connective tissue and some muscle has been removed the vertebrae are exposed *in situ* as shown).

nus (Macruronidae) as a composite unit incorporating an accessory neural arch suggesting that the first centrum had been incorporated in the 'basioccipital'. Since, however, 1) ribs are always lacking from the first two vertebrae in gadiforms, 2) Baudelot's ligament always occurs on the first centrum and 3) an accessory neural arch does not occur above aulopiforms, it seems untenable that incorporation has occurred in macruronids.

The caudal fin skeleton is lacking in the majority of gadiform taxa but where it does occur its most significant features are fusion of the upper hypurals and the presence of X and Y bones (lost in some taxa, see above), both of which contribute to the symmetry characteristic of 'supragadoids'. The morid caudal fin skeleton is regarded as the plesiomorphic gadoid type since it approaches that of most other teleosts in its asymmetry and in having distally separated hypurals. In this latter respect, *Melanonus* demonstrates a further derived condition in having the hypurals distally fused (see further discussion on p.30).

Of particular note is the condition of the caudal fin musculature (Fig. 15C) which differs from that described in gadoids (Howes, 1991) where *hypochordal longidorsales*, *flexores dorsales* and *inferiores* are absent, the *interradiales* have a characteristic linkage pattern between the caudal fin rays and are continuous with the dorsal and anal fin rays. Howes (1991: 104) pointed out the absence of the latter in Melanonidae, but overlooked the fact that the caudal fin musculature more closely resembles that of other paracanthopterygians and acanthopterygians in having discrete dorsal

and ventral *flexores* and an amalgamated segment of *interradialis* musculature corresponding to the superficial *interradialis*.

Melanonus, *Lyconus* and *Brosme* are the only gadiform taxa to possess a single dorsal fin, most have two and the more derived Gadidae have three. Dorsal fin origin is usually above the second and third neural spines, as in *Melanonus*, but the origin of the second dorsal is variable, the radial supporting the first ray of that fin being between the eighth and ninth, ninth and tenth or tenth and eleventh neural spines. According to Inada (1989) the single dorsal fin of *Lyconus* evolved from amalgamation of two separate fins. Inada's evidence relies on a notch being present in the fin at a point above the proximally curved thirteenth radial which lies between the eighth and ninth neural spines which as just noted is the region commonly associated with the origin of the second dorsal fin. No similar 'evidence' occurs in *Melanonus*.

Among gadoids the first radial of the first dorsal fin usually lies between the second and third neural spines, but this is variable being between the first and second in gaidropsarids, and in Bregmacerotidae the first radial has become directed forward so that the first dorsal fin ray lies above the supraoccipital. In macruronids, the first supporting radial is also usually between the second and third neural spines but sometimes between the third and fourth. Percopsids, like melanonids have the first radial between the third and fourth neural spines. In ophidiiforms the position of the first radial is variable and can lie between any of the neural spines from the

first to the tenth. In batrachoidiiforms it is usually between the third and fourth neural spines and in lophiiforms the eighth and ninth or more posterior neural spines.

Supraneurals, preceding the first dorsal fin are rarely present in gadiforms (Patterson & Rosen, 1989).

Baudelot's ligament (Figs 13A,B) stems from the lateral cavity of the first vertebra to connect with the supracleithrum. The *retractor dorsalis* muscle originates from the fourth through sixth vertebrae; on the sixth it is attached to the leading edge of the parapophysis (Fig. 13B).

Brain (Fig. 16).

The brain of *Melanonus* is situated well forward, the telencephalon and anterior part of the mesencephalon being anteriorly displaced beyond the cranial cavity so as to lie in the orbital cavity formed by the enlarged pterosphenoids. The olfactory and optic lobes are large. The olfactory tracts are well separated and each tract is short and thick comprising at least twelve separate nerves each of which branches to

feed the individual laminae of the nasal rosette. The olfactory bulb is large and lies against the lobe which is narrowly separated by a fissure from the laterally situated optic lobe. Upon leaving their respective lobes ventrally, the optic tracts cross and travel directly laterad a short distance to the eyeball which is only narrowly separated from the telencephalon. The cerebellar corpus is flat and lies pointing anteriorly between the optic lobes. This is a unique condition among gadiforms (noted by Marshall & Cohen, 1973 as diagnostic of the Melanonidae), normally the corpus is bulbous and elevated (Okamura, 1970) or lies posteriorly along the cerebellar crest. The cerebellar crest is flat and elongate flanked ventrolaterally by extensive trigeminal lobes. The cerebellar body extends posteriorly to entirely overlap the vagal lobes along the basal part of the medulla oblongata, also a unique gadiform condition. The granular eminence is large but not laterally extended. Ventrally, the inferior lobes, pineal body, hypophysis and vascular sac are all well-developed.

The brains of some gadoids and macrouroids have been described by Svetovidov (1953), Okamura (1970) and Howes

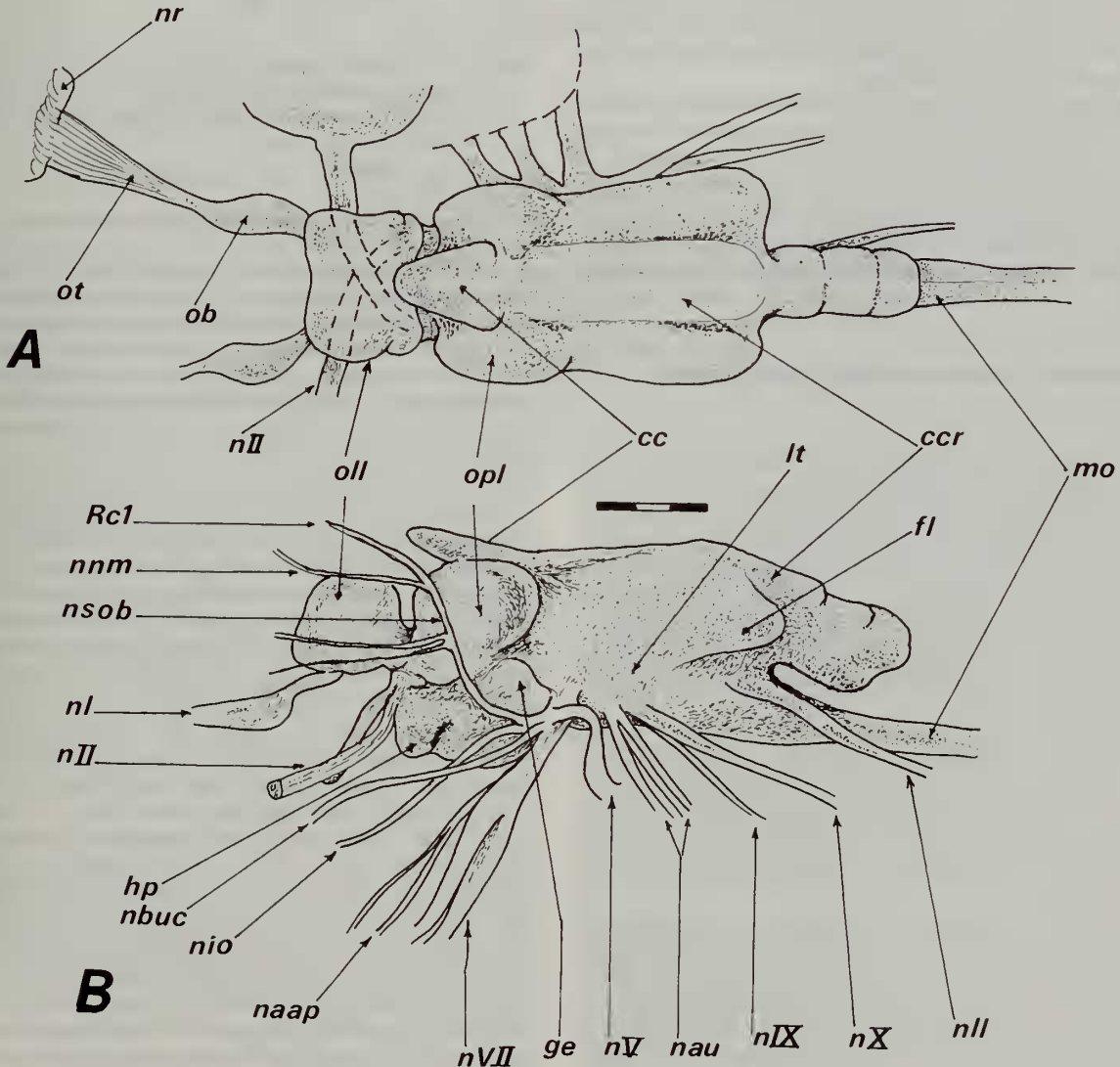


Fig. 16. *Melanonus zugmayeri* brain in A, dorsal and B, lateral views. In A, the pathways of the optic tracts beneath the lobes are indicated by dashed lines and the margin of the prootic is indicated by dashed lines lateral to the trigeminal-facial nerve complex.

& Crimmen (1990) and of those published descriptions *Bregmaceros* has the most similar overall morphology. Like that of *Melanonus* the brain is elongate with extensive trigeminal-facial lobes, a long cerebellar crest and closely connected olfactory bulb and lobe. However, there are major differences in the relatively small size of the olfactory and inferior lobes and in the cerebellar corpus being orientated posteriorly along the crest, having a posterolateral fissure and leaving the midline of the optic lobes exposed.

Anterior placement of the forebrain was considered a gadiform character by Svetovidov (1948) and among gadoids there is a tendency for the brain to be shifted forward. In those few morids investigated and in macrouroids the forebrain is generally confined to the cranial cavity. In some other paracanthopterygians (ophidiiforms, Howes, 1992 and percopsids pers. obs.) the telencephalon lies in the orbital cavity as in *Melanonus*.

It is problematic as to which features of gross brain morphology can be used as phylogenetic markers. The degree of separation of the olfactory bulb from the lobe is variable in gadiforms (discussed by Howes & Crimmen, 1990) but the plesiomorph condition, possessed by *Melanonus*, is seemingly for them to be closely associated. The shape of the olfactory lobe is also a highly variable feature and one that might, at least, be generically characteristic.

Summarising data from gadoid brain descriptions given by Svetovidov (1953) it appears that elongate and short cerebral crests are equally distributed amongst the taxa he studied. A short, tall cerebral crest, common to gadoid brains, is also the common condition among paracanthopterygians. However, the granular eminence, although often large is laterally extended only in the Gadidae (*sensu* Dunn, 1989 and Howes, 1991b).

Swimbladder, viscera and body musculature (Fig. 17).

The *swimbladder* is an elongate ellipsoidal, thin-walled sac adhering tightly to the vertebral column apart from where the long bilobed *kidney* runs on either side of the midline. According to Marshall & Cohen (1973) the melanonid swimbladder is reduced and there are two retia. In the specimens of *M. zugmayeri* examined for this feature, the gas-gland covers nearly two-thirds of the anterior floor of the sac and there are four retia supplying separate lobes. Posteriorly the gas-gland tapers and is deeply pocketed. The oval appears to be beneath the retial area.

The *stomach* is siphon-shaped, exceptionally thick-walled with a deeply and much convoluted mucosal membrane; there are six or seven caeca lying ventrally; the *intestine* is long and double-banded. The bilobed *kidney* is extensive, almost enveloping the stomach. The *gonads* lie posteriorly on either side of the swimbladder to which they are attached by thin strands.

The *anterior body musculature* is similar to that described for Bathygadidae (Howes & Crimmen, 1990) except that melanonids lack the same degree of differentiation between dorsal and ventral sections of the *epaxialis* musculature (Fig. 17), the dorsal section being apparent only anteriorly (the general condition) and not extended as far posteriorly as in bathygadids.

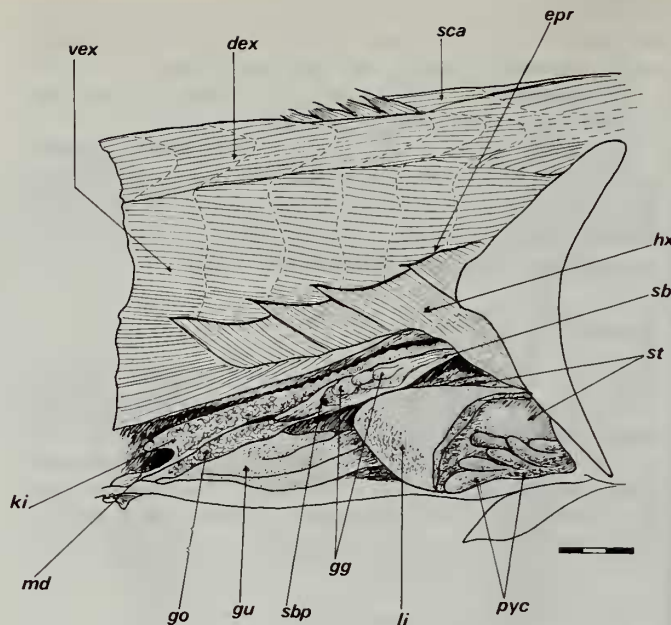


Fig. 17. *Melanonus zugmayeri* anterior body musculature and visceral cavity dissected on the right side; the anterior part of the liver has been cut away to expose the pyloric caeca and the swimbladder has been dissected.

DISCUSSION

Melanonus has undoubtedly derived sensory features; the brain has a unique morphology amongst paracanthopterygians, extending well forward into the orbital cavity, the head is covered with a unique type and pattern of open-ended neuromasts innervated by the ramus canalis lateralis of the trigeminal nerve, the RLA nerve being absent. In its cranial osteological characters three can be considered derived: the shape of the fifth infraorbital, and exclusion of the supraoccipital from contributing to the foramen magnum. The first two of these osteological characters are autapomorphic; the enlarged pterosphonoid is undoubtedly correlated with the anterior position of the telencephalon. The third is a feature shared with ophidiiforms, in that group, however, the exoccipital is expanded dorsoposteriorly so as to exclude most of or the entire supraoccipital from the rear of the cranium and from contact with the first neural spine. In melanonids the supraoccipital is excluded from the border of the foramen magnum by its failure to extend ventrad during development, but nevertheless it still forms the upper posterior border of the cranium and contacts the first neural spine.

Aside from these autapomorphies there are no other apomorphies which are shared with other gadoid taxa. The diagnosis of 'Gadoidei' has proved difficult since most synapomorphies so far proposed are either not exclusive to, or their distribution has not been completely documented, in the taxa currently embraced under this category (see below).

Howes (1990; 1991a; 1991b) proposed a series of gadoid clades of which 'supragadoids' were recognised on the basis of a fused upper hypural plate of the caudal skeleton. A sequence of other synapomorphies, including an interopercular fossa, contact of the posterior face of the lateral ethmoid wing by the first infraorbital and reduction of pterygoid bones (Howes, 1990) excluded Melanonidae from this group. Other

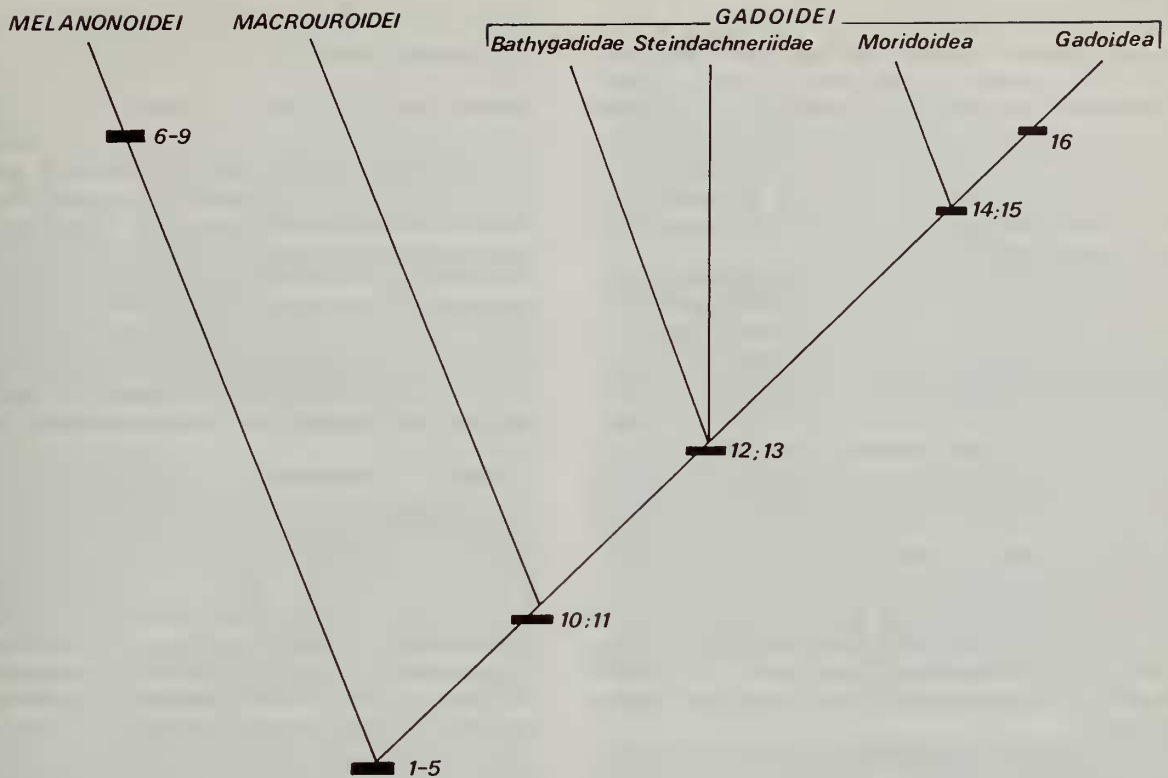


Fig. 18. Proposed relationships of Melanonoidei with other gadiforms. *Synapomorphies*: 1, absence of pars jugularis, i.e. common aperture for principal cranial nerves (also occurs in some ophidiiforms); 2, loss of intermusculars from vertebrae 1 and 2; 3, scapular-coracoid foramen; 4, attrition of lateral face of hyomandibular; 5, *levator arcus palatini* covers lateral face of jaw musculature; 10, palatine forming a hinge or butt-joint with pterygoids; 11, enlarged intercalar contributing to posterior wall of cranium; 12, pharyngohyoideus muscle mediated by sternohyoideus; 13, interradiales muscle connected to dorsal and anal fin rays, loss of various caudal fin muscles and entire caudal skeleton in some taxa; 14, palatine contacts mesethmoid; 15, X and Y bones in caudal skeleton (lost in some taxa); 16, complete fusion of upper hypurals and symmetry of hypural plates. *Autapomorphies* for Melanonoidei; 6, supraoccipital excluded from margin of foramen magnum; 7, cranial neuromast pattern and innervation; 8, brain position and morphology; 9, enlarged pterosphenoids contacting lateral ethmoids. *Synapomorphies* 1-5 and 10-11 from Gosline (1968; 1971); Howes (1988; 1989; 1990; 1991b); Markle (1989); Patterson & Rosen (1989). *Synapomorphies* for macrouroids summarized by Iwamoto (1989) and Howes & Crimmen (1990) and for moridooids by Paulin (1983).

taxa so excluded are Moridae, Euclichthyidae, Steindachneriidae and Bathygadidae. The two latter lack a caudal fin skeleton, thus the incomplete fusion patterns of hypural bones possessed by morids, euclichthyids and melanonids cannot be extended to these taxa. The cranial and vertebral osteology of Bathygadidae is plesiomorphic in comparison to other gadoid taxa whereas that of Steindachneriidae is relatively derived (pers. obs. see also Fahay's, 1989, notes on pelvic girdle morphology).

The Melanonidae lacks a feature common to other gadiforms (macrouroids + gadoids), namely, a short palatine forming a butt or hinge joint with the ento- and ectopterygoids. In almost all gadiforms the palatine has a truncated near vertical margin which forms a mobile (laterally expanding) joint with the anterior margins of the pterygoid bones (p.20). *Melanonus* has a plesiomorphic palatine where the stem firmly contacts the margin of the ectopterygoid. Moreover, the palatine extends some distance along the ectopterygoid and is toothed. Since no other gadiform has palatine teeth it might be assumed that the melanonid palatine is the primitively composite dermo- and autopalatine whereas other gadiforms have lost the dermal component. In other paracanthopterygians, ophidiiforms and lophiiforms possess the plesiomorphic, long posteriorly extended and toothed palatine;

percopsids resemble gadiforms more closely in having an edentulous bone which abuts the straight anterior margins of the ecto- and entopterygoids but which still retains a posteriorly directed stem (p.20).

The Melanonidae possesses three of those characters identified by Patterson & Rosen (1989) and Markle (1989) as gadiform synapomorphies or potential synapomorphies, namely, absence of epipleural ribs from the first and second vertebrae; a scapular-coracoid foramen and absence of a lateral commissure, cranial nerves I-VII exiting through a common aperture. Two other potential synapomorphies listed by Patterson & Rosen (1989) are presence of X and Y bones and liver LDH pattern. X and Y bones are absent in melanonids and can only be judged as a plesiomorphic state or, against the congruence of other synapomorphies, as secondary loss. In the latter case the feature then appears as synapomorphic for a subgroup of gadoids (Fig. 18). LDH liver pattern has not been tested for in this taxon.

Two other synapomorphies appear to be: 1) the form of the hyomandibular, which in the majority of gadoids and macrouroids has attrition of the anterior border and lateral face, fully or partly exposing the pathway of the hyoid branch of the facial nerve (Howes, 1989; 1991b; 1992); 2) the *levator arcus palatini* covering the *adductor mandibulae* musculature

laterally (Howes, 1988; 1991b).

Melanonids have a small intercalar, a bone which in other gadiforms contributes to a substantial part of the lateroposterior cranial wall. In size the melanonid intercalar approaches that of *Percopsis*. Whether in *Melanonus* the bone is plesiomorphically small or whether there has been reduction secondarily can only be assessed against the distribution of other, known derived features (Fig. 18). An intercalar is absent in lophiiforms and batrachoidiforms, an assumed secondary loss (Patterson & Rosen, 1989).

The single dorsal fin is probably a plesiomorphic feature (p. 26). Among paracanthopterygians, an elongate second dorsal fin is assumed to be synapomorphic for anacanthines (*sensu* Patterson & Rosen, 1989). Melanonids share with ophidiiforms (including carapids and bythitoids), two gadoid genera (*Lyconus* and *Brosme*) and Macrouroididae a single dorsal fin which must be seen as resulting from either the 'loss' of the first dorsal with anterior encroachment of the second, or the amalgamation of the two fins. It is impossible to distinguish between such phylogenetic events although either way the condition is seen as derived. Iwamoto (1989) considered the single dorsal fin of macrouroidids to be derived but that of the gadoid *Brosme* as plesiomorphic retention. Judging by the incongruent distribution of the character it is almost certainly homoplastic. The further partitioning into three fins in Gadidae represents a further derived state.

In jaw musculature melanonids are little different from morids and bathygadids (Howes, 1988). Howes (1990; 1991b) noted a medial shift of adductor muscle A1b which would suggest a close phylogenetic relationship with supragadoids. This shift, however, is apparently induced by the presence of a unique transverse ligament which runs from the palatine to the inner face of the second infraorbital and which constricts and turns A1b inwards. This is not the same condition as the entire medial shift of an unconstricted A1b in 'supragadoids'.

Melanonids have an unusual condition of the hyoid musculature whereby the *pharyngohyoideus* (= *rectus communis*) attaches to the third hypobranchial as well as the urohyal (Howes, 1988). Urohyal attachment of the *pharyngohyoideus* is shared with macrouroids, two gadoid families and all other ctenosquamates (Lauder, 1983; Howes, 1988); in remaining gadoids the *pharyngohyoideus* is mediated by the *sternohyoideus*. It is assumed that the two exceptional gadoid families (Muraenolepididae and Ranicipitidae) have lost the *sternohyoideus* attachment, the *pharyngohyoideus* being attached to the tip rather than the lateral face of the urohyal keel as it is plesiomorphically in melanonids.

The melanonid caudal fin musculature (p. 26) lacks those features regarded as synapomorphic for gadoids (since macrouroids lack caudal fin skeletons and associated musculature it cannot be known whether this derived form of muscle arrangement was a gadiform feature subsequently lost in macrouroids). Melanonids have a caudal fin muscle arrangement only slightly modified from that present in other paracanthopterygians and in acanthopterygians.

Although it cannot be doubted that the Melanonidae belongs among Gadiformes there is no evidence to suggest that it be regarded as a member of the Gadoidei. To be included within the Gadoidei, the elongate toothed palatine, lack of X and Y bones, reduced intercalar and single dorsal fin must be regarded as reversal and loss characters. The caudal fin skeleton demonstrates an advanced condition to that of the Moridae (the plesiomorphic gadoid taxon) in

having, in adults, almost complete fusion of the upper hypurals which alone, would signify inclusion within the 'supragadoids'. Indeed, I have argued elsewhere (Howes, 1991b: caption to fig. 35) that the reported separation of hypurals in young ranicipitids (which I place amongst the 'supragadoids') is a character reversal; a conclusion drawn on what appears to substantial support from other synapomorphies. In the case of melanonids the principal evidence against the caudal fin skeleton being a character reversal is that the associated musculature has a plesiomorphic arrangement, lacking those derived elements found in the musculature of morids and other gadoids, including ranicipitids (as an adult, *Raniceps* has the typically symmetrical gadoid caudal fin skeleton, lacking in *Melanonus*). Thus the fusion or partial fusion of the upper hypurals in melanonids is considered to have occurred independently to that in gadoids above the morid level.

Taking into account these arguments and the anatomical evidence presented herein, the Melanonidae is regarded a basal gadiform taxon, representing, as Markle (1989) had previously hypothesised, the sister-group to both gadoids and macrouroids (Fig. 18). Such a phylogenetic arrangement leads to a higher level re-classification of the Melanonidae. Following Markle (1989) and recognising the family as being phylogenetically coordinate with the Macrouroidei and Gadoidei, it is placed in the suborder Melanoidei. Those taxa which I have previously recognised as a monophyletic group termed 'supragadoids' are equivalent to Markle's (1989) Superfamily Gadoidea. The Moridae and Eulichthyidae are regarded by Markle (1989) as sister taxa on the basis of asymmetry of procurrent caudal fin rays; I know of no supporting osteological synapomorphies for this relationship but provisionally accept it. Together these taxa form the sister-group to the Gadoidea and as such must be regarded as the Superfamily Moridoidea (= Moriformes, part, Schwarzhans, 1984). The 'infragadoids', Steindachneriidae and Bathygadidae have no such status since they form an unresolved polychotomy with the Gadoidei + Moroidei and Macrouroidei.

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